



GROWTH AND ASEXUAL REPRODUCTION IN CORALS

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WITH FOURTEEN TEXT-FIGURES, TEN PLATES, AND NINE TABLES

CONTENTS.

	PAGE
PREFACE	167
MATERIAL AND METHODS	169
THE RESULTS OF THE PRINCIPAL EXPERIMENT	174
THE RESULTS OF SUBSIDIARY EXPERIMENTS	183
BUDDING IN ASTRAEID CORALS	190
THE RELATION BETWEEN FORM AND ENVIRONMENT IN CORALS	200
SUMMARY AND CONCLUSIONS	207
TABLES OF MEASUREMENTS	209
REFERENCES	216
SYSTEMATIC INDEX	217

PREFACE.

THE field work which formed the foundation for the results described in this paper was carried out by T. A. Stephenson, with the assistance, in the early stages, of F. W. Moorhouse, and later on of the natives Harry, Paul and Stephen, with incidental help from other sources. The photography was also done by T. A. Stephenson, with assistance in the development of films, at the end of the experiments, from M. A. Spender. Since our return from Australia the whole of the measurements have been made by Anne Stephenson, who has also enlarged a great many of the photographs and taken a large share in the preparation of both text and figures. We wish to thank everyone who helped us in the execution of a laborious piece of work, and especially F. W. Moorhouse, whose assistance at the beginning was invaluable ; and E. A. Fraser, whose notes and collections made on the Outer Barrier considerably extended the scope of our study of forms of growth in corals.

We are indebted to F. Pittock for photographs taken from collected material ; and to S. M. Manton for the loan of three negatives, and for the specimens illustrated in Plate X, figs. 1 and 2. Prof. Matthai has very kindly identified many specimens for us, and the names here used are based on his determinations in most cases. A few species have been identified by T. A. Stephenson. The mollusca mentioned on p. 215 were identified by Mr. J. R. le B. Tomlin.

The question of growth-rate among corals has already received a considerable amount of attention, and experiments of some magnitude have been carried out by Vaughan (1916), Mayor (1924), and Edmondson (1929) in particular. Vaughan deals with Atlantic reefs, Mayor with Samoa and Fiji, and Edmondson with Hawaii. A series of observations from the Australian Barrier Reef therefore supplements these very suitably. With the addition of these new observations, we have now enough information to give us a fairly good idea of the way in which coral behaves in various parts of the world ; but it will be only too evident to anyone who reads these pages that even now the gaps in our knowledge are numerous and sometimes wide. All the work mentioned when put together does not deal with a really large number of coral colonies. This is bound to be the case, from the very nature of the problem ; experiments on a definitely large scale, often involving much transportation of heavy corals, could only be performed by teams of workers such as have not yet been available. Those which have so far been completed, however, serve to suggest lines of work which we hope will yet be followed up with profit.

We do not propose to give a history of what is known about coral growth. This has already been done, and the principal facts are reviewed in the papers mentioned in the last paragraph.

The main object of our experiments was to ascertain the normal rate of growth of a selection of different kinds of coral, belonging to the several growth-forms (massive, branched, etc.), which commonly occur upon reefs. We record here also the outcome of some subsidiary experiments, the results of which proved to be very interesting, although their scale was, by force of circumstances, much smaller than that of the principal experiment.

This series of experiments formed part of a programme of ecological work which was directed towards discovering the nature and distribution of the population of the Low Isles Reef, in relation to the several habitats available there, and its relation to the physical and chemical conditions prevailing in these habitats. A general account of the reef and its organisms has already been published (No. 2 in this volume) ; the present paper forms a second contribution to the subject, and reports dealing with other aspects will follow.

We suggest to future investigators that the following lines of work would repay further study. Along some of them a considerable amount of work has already been done ; in other cases the field is almost untouched. The results recorded in the present paper will give some indication of the way in which such investigations might be expected to develop.

(1) An ecological comparison of coral habitats : The amount of growth which a coral achieves during a known period of time (if a sufficiently long period be allowed) may be taken as giving some index to its condition. It should therefore also give some indication as to the suitability of the habitat in which the coral is living, as a *milieu* for that particular coral species, provided always that due allowance be made for the operation of certain factors which affect its growth (see p. 174). In other words, the relative favourability of habitats may be compared by using corals judiciously as indicators. It is also

possible to compare the productivity of different parts of a reef (on the lines of Gislén's work on the epibioses of the Gullmarfjord), if the weights of skeleton deposited, and of coral tissue produced, are ascertained during the course of an experiment.

(2) A comparison of the normal growth-rate of a coral with the rate of regeneration in the same species, under various circumstances.

(3) A study of the changes in symmetry which take place in a colony as it develops. The normal course of the development of its characteristic shape should be ascertained, from the time of settling of the planula onwards, under circumstances which permit the coral to grow freely on all sides. This should be compared with the behaviour of corals which have at first been prevented by their surroundings from developing a normal symmetry, and which are subsequently transplanted to an environment where free extension in all directions is possible. Other comparisons in this sense will readily suggest themselves.

(4) A study of the growth-curves of coral colonies and species from the time of settling of the planula to the adult condition; with reference not only to the rate of development of the colony as a whole, but also to the behaviour of the ratio between the rate of deposition of skeletal material and the rate of increase in weight of the soft parts.

(5) Further investigation of the processes of asexual reproduction in corals, ascertained by direct observation on the living polyps.

(6) Further study of the problem of species among corals, both in the field and by means of experiment.

MATERIAL AND METHODS.

MATERIAL.—This report deals with the activities of 246 corals, all of which, with three exceptions, were collected at Low Isles. The exceptions came from Batt Reef. The Low Isles material was all collected either in the anchorage or in the Western moat.*

THE MEASUREMENT OF CORALS.—The difficulties involved in making accurate measurements of corals are realized only when an attempt is made to do it. Many corals are very irregular in shape, and in the case of branched forms this makes the measurement of a circumference, for instance, unsatisfactory. The measurement of diameters with a tape is also unsatisfactory. Diameters may be measured with calipers, but here the difficulty arises that it is necessary to mark in some way the diameter which one has measured. This may be done in the case of massive corals by driving small nails into them; but this is not, in practice, easily performed in a satisfactory manner, and has the disadvantage that it may induce abnormality at the very point where normality is most desired. In the case of branched corals, one may mark the branches at the ends of the diameter with wire. In such a case it is quite possible that the marked branch will be injured during the experiment; and in many branched forms it is actually impossible to get one's fingers between the branches, because they are too close together. Further, if the coral is to be marked *in situ* the measuring will frequently be complicated by the awkward shapes of surrounding rocks and corals, and, if the coral is in shallow water, the surface ripples which occur on most days in the year will render it impossible to see clearly what one's fingers are doing beneath the surface.

* These localities may be identified by reference to the key chart of Low Isles given in Report No. 2 in this volume, Text-fig. 2. Batt Reef lies some 7 miles to eastward of Low Isles.

We proved the truth of these objections by trial ; and as a result, evolved a method whereby the coral to be measured would be twice photographed, once at the beginning and once at the end of the experiment, and the measurement could be made on the negatives. The method is somewhat elaborate, but gave excellent results. We describe it in the following paragraphs in the hope of helping future workers ; because we should have been most grateful, when we started our experiment, if we had possessed more details of the methods of our predecessors.*

THE EXPERIMENTS.—Four experiments were carried out, as follows :

Experiment I.—In this case 169 corals were used. They were attached by means of cement to 100 blocks of concrete, which were planted out on the reef in suitable places after the corals had been photographed. In this experiment all the corals whose measurements are recorded, with two exceptions, were planted out in pools situated within 100 yards of the localities from which they were collected.

Experiment II.—Here 11 colonies were used, each colony being divided into halves. The halves were mounted on 10 concrete blocks, which were planted out on the reef as before ; but in this case one half was placed in its natural environment, the other in an environment alien to it.

Experiment III.—In this case 30 colonies were marked *in situ*, by a diver working below the level of low water.

Experiment IV.—Clean materials of various kinds (p. 188) were fixed at several points on the reef, in the hope that coral planulae would settle upon them. Thirty-six young colonies were obtained in this way.

CONSTRUCTION OF BLOCKS.—The concrete blocks used in Experiments I and II were made from sand and cement (3–5 parts of sand to 1 of cement) mixed with sea-water. The mixture was poured into a series of moulds formed by a frame consisting of eight detachable lengths of wood, fitting into one another in such a way as to bound nine rectangular cavities. The bottoms of the moulds were formed by a sheet of galvanized iron on which the frame rested. The size of the blocks so produced was about 11 in. by 10 in. by 2 in. On each block, while the cement was still soft, a number was impressed ; and two holes were made through it by the insertion of glass tubes wrapped in well-greased paper. These tubes were removed after the cement had set, and through the holes thus left large iron spikes were driven when the block was subsequently attached to the reef. The blocks were left in the moulds overnight, and were watered to prevent too rapid drying ; the next morning they were removed and trimmed, placed in the sea, and left there to “cure” for two or three weeks.

ATTACHMENT OF CORAL.—The corals collected for attachment to the blocks were all healthy specimens, and examples of reasonably symmetrical form were chosen where possible. Colonies of various sizes were used, but there was an upward limit imposed by the difficulty of transporting any colony exceeding a certain weight. The corals were subjected to as little exposure as possible ; they were brought up from the reef in buckets of water, and attached to the blocks, in a shady place, with a mixture of pure cement and sea-water of about the consistency of plasticene. The cement was allowed to set for about 10 to 15 minutes, after which coral and block were returned to the sea. By the next

* Our method gave information only as to increase in diameter and change in form of the coral as seen from above. We should have liked to record increase in height and weight also, but had neither the time nor the apparatus required for this.

morning the cement had set quite firmly, and the coral, if still healthy, could then be photographed and afterwards planted out in a suitable place on the reef. When collecting the corals prior to their attachment to the blocks, specimens were obtained, wherever possible, which could be removed from the reef with a piece of the rock on which they had been growing still attached to their bases. This prevented any direct contact between the cement and the living tissues of the coral.

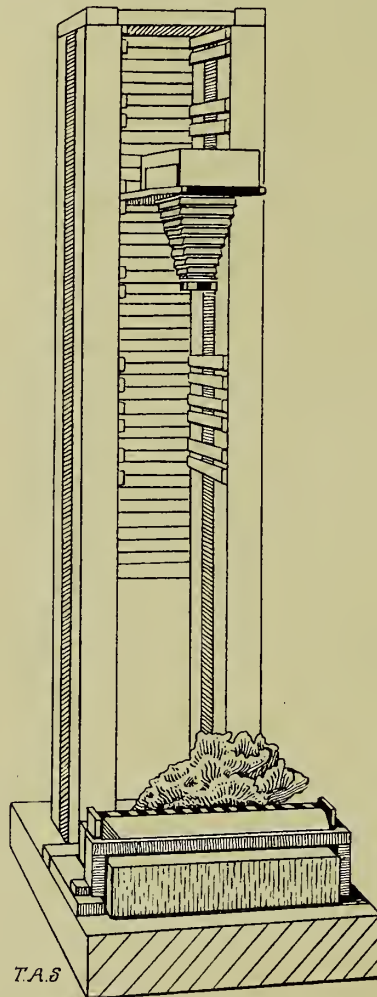
CONSTRUCTION OF PENS.—The number of people who had access to the reef, at low water, made it impossible to plant out experimental corals without protecting them in some way. We therefore decided to make two pens or enclosures, each containing a large pool surrounded by growing coral, and to plant out the blocks in these pools. The pools were therefore fenced in, the fences consisting of mangrove stakes driven into the reef with a sledge-hammer (a hole had to be made first with a six-foot crowbar), and laced together with stout wire. Since the floors of the pools were sandy, it was also necessary to make some provision against a silting-up of the experimental corals. This was accomplished firstly by arranging large boulders round the edge of the pool, and secondly by paving such parts of its floor as were not covered by cement blocks with flat slabs of beach-sandstone. All these paving materials had to be held in position by additional stakes and wiring; and the cement blocks themselves by means of 10-in. iron spikes. Even then the movement of sediment in one of the pools threatened to bury the blocks, and this was overcome by making a second series of blocks and mounting the first on top of them.

One of the pens was situated in the Western moat—a place in which the water was only just deep enough to cover the corals completely, during the period of low water. The physical and chemical conditions prevailing in this moat are described briefly in the general ecological report in this volume (No. 2, pp. 45–46), and will be dealt with in more detail by A. P. Orr in another report. We need, therefore, only say here that the conditions are those of a shallow tidal pool which may become very warm during low water, and which forms an environment unfavourable for the growth of many corals, although suited to that of a few species. The second pen was situated in the anchorage, in a place which was open to the sea at all states of the tide, and which became shallow enough to be visited on foot during low spring tides, but was at other times accessible only to a diver. The conditions were thoroughly favourable for a varied growth of coral, and the extremes liable to occur in the moat were largely eliminated. This environment also has been described in the ecological report (pp. 61–64), and will receive further attention from Orr.* The two pools, therefore, formed a contrast to one another, one representing a much more generally favourable environment than the other.

PHOTOGRAPHY.—It was necessary to construct some apparatus by means of which we could ensure that the two photographs of each coral, taken at the beginning and end of each experiment, should be taken from exactly the same angle. For this purpose the structure illustrated in Text-fig. 1 was made to our design by F. W. Moorhouse. It consisted of four strong wooden uprights, rigidly attached to one another, at the foot of which lay a horizontal platform upon which the cement block could be placed, the platform being firmly fastened to the uprights. Two wooden guides, raised above the platform, ensured that the block should occupy exactly the same position on it both before and after the experiment. That the camera should hold exactly the same relation to the block

* The temperature of the water in the anchorage was also ascertained twice daily, throughout the year, by F. W. Moorhouse. These observations will be published in another report.

on both occasions was also arranged by placing it, facing downwards, between the arms of a specially constructed wooden shelf which slid into a groove between the four upright pillars. Several such grooves were made, and were numbered, so that if need be the camera could be used at different distances in the case of different corals. A scale was introduced into the photographic field in the following way: A small wooden bridge was constructed, which could be placed astride the cement block, and could be replaced in a known position by means of guides, as in the case of the block itself. On the upper side of the bridge were fixed (1) a glass ruler on which had been painted approximate square



TEXT-FIG. 1.—Diagram of the apparatus used for photographing corals. This apparatus is described on pp. 171-2. Some of the details have been simplified or omitted in the diagram, in order to make clear the general arrangement of parts.

centimetres, and (2) an accurate slide-rule with its edge facing the camera. The photographs were taken with the smallest available aperture (F36), in order to ensure an adequate depth of focus, the camera being actually focused on the ruler. The results were satisfactory; the finest divisions of the slide-rule were sharply recorded on the negatives, and excellent definition was obtained in the outlines of the coral.

PROGRESS OF THE CORALS DURING THE EXPERIMENT.—Experiments I and II were started in September, 1928, and ended in May, 1929. When the corals had once been established in the pens they required no attention beyond periodic inspections, during which any dead colonies were removed, and details were noted of any sick or injured specimens. Unduly troublesome pieces of debris or accumulations of sediment, or algae, which had caught in the branches, were removed at such times. For the most part the condition of the corals remained excellent in both pens throughout the experiment. The number which died or were too much broken for re-measurement was 36 in a total of 180—20% of the whole. A number of the casualties were due to the blundering activities of large fish which from time to time visit such pools.

On 28th February, 1929, after heavy rains, flood-water from the Daintree River (the mouth of which lies a little to the north of the reef on the adjacent mainland) swept a large amount of mud and debris into the sea. The effect was so marked that the sea all round the reef became peaty-brown in colour, and partially opaque. When the pen in the moat was visited on the next day the corals were not visible at all in 3 ft. of water. On 4th March the water had cleared and the corals were examined. A large amount of flocculent sediment had collected, but apparently with little ill-effect. A number of deaths had occurred, but the dead specimens were all more or less brown and covered with algæ, which means (see p. 205) that they probably died *before the flood*. The cause of their death, we believe, was a spell of unusually hot weather coinciding with spring tides, which had preceded the flood, and during which a number of coral deaths on the reef outside the pens had been noted.

On 22nd April, 1929, a large proportion of the corals in the anchorage pen were found to be covered with an extensive growth of beard-like Cyanophyceæ (of a type similar to *Lyngbya majuscula* or *Hormothamnium solutum*), some specimens being almost hidden by it. This growth had come into being during the preceding three or four weeks, and seemed to be generally prevalent in the anchorage.

As we had no knowledge as to what effect these smothering algae would have on the corals, the experiment was ended on the next day.

PROCEDURE IN EXPERIMENTS III AND IV.—The method above described applies to Experiments I and II, and that used for no. IV is described on p. 188. In Experiment III, where the corals were marked *in situ*, a different method was adopted. A. In a number of colonies the ends of individual branches were broken off, each broken branch being marked with a ring of silver wire, and each colony with a silver label bearing a stamped number. The object of this procedure was to obtain data respecting the regeneration of the broken branches. In the cases of other colonies, where the branches were too close together to permit of convenient individual marking, a loop of silver wire was tied round the bases of a group of branches, and all the branches within the loop were broken. B. There are certain species of *Acropora* which form shelf-like or cyathiform colonies, in which the branches on the upper surface are all fairly even in length. It occurred to us that if we killed some of the branches in such corals, by placing a cap of plasticene over their tips, we should be able to ascertain approximately the amount of growth of the undamaged branches, by noting the difference in level between the living and dead branches, after a suitable period had elapsed. This method would probably give good results if carried on long enough; but in our own case we tried it too near the end of the time available, and the amount of growth which occurred was not enough to give a satisfactory result.

THE RESULTS OF THE PRINCIPAL EXPERIMENT.*

(EXPERIMENT I.)

(The Growth of Corals Mounted on Cement Blocks, in their Natural Environment.)

A. FACTORS WHICH AFFECT CORAL GROWTH.

In considering the results of the experiments, a number of factors which may be expected to exert some influence on coral growth must be considered. The factors in question are the following :

(1) INCONSTANCY OF GROWTH RATE.—It was noted by Wood-Jones (1910, p. 69) that corals do not necessarily grow at an even rate, but may increase by fits and starts. He showed that one coral might grow rapidly for a time, and make no further progress in the succeeding period ; whilst a neighbouring colony might be quiescent during the period within which the first had been active, and grow again while the first was in its passive phase. Such periods may alternate with one another irregularly, and have no connection with any known cause. These observations were confirmed by Mayor (1924, p. 52) and Edmondson (1929, p. 20). The experiments described in this paper do not add further evidence on this count directly, since each coral was measured twice only ; but an analysis of the figures shows that the exact length of the experiment bears no direct relation to the amount of growth achieved, and that its exact duration affects the amount of growth recorded less than any of the other factors involved. This result is doubtless to be ascribed, in part, to the effects of an erratic rate of growth, and may be regarded as an indirect confirmation of the conclusions of previous workers.

This irregularity of increase renders the interpretation of results distinctly complicated ; one must constantly be on the watch for effects which may be due to it, and it is not always possible to distinguish such results from those which are in reality due to other causes. In the following sections an attempt is made to evaluate some of the other factors which undoubtedly contribute to the determination of the amount of the growth which a coral will make, but it must be remembered that the intermittent nature of the growth will complicate these discussions in greater or lesser degrees. It seems to be clear, however, that apart altogether from the influence of the spasmodic rate, there are other recognizable effects due to environment and to the age of the coral. Although the figures bearing on these latter factors are complicated by the former, the results of the several influences can be disentangled fairly easily. In the case of individual variation the separation of effects is more difficult, but even here both the individual variation and the uneven growth-rate appear to contribute to the actual result.

In the present experiments the period of growth allowed to the corals was not quite the same for all of them. Sometimes it was the same for any two colonies, or differed only by a few days or a week ; in other cases there was a difference of several weeks. In the case of those corals which were kept in the anchorage the maximum variation in period of experiment between any two of them was 25 days ; in the moat the maximum was 30 days. Only when moat and anchorage corals are compared with one another (and this comparison is rarely made) does any question of a discrepancy of more than a month arise.

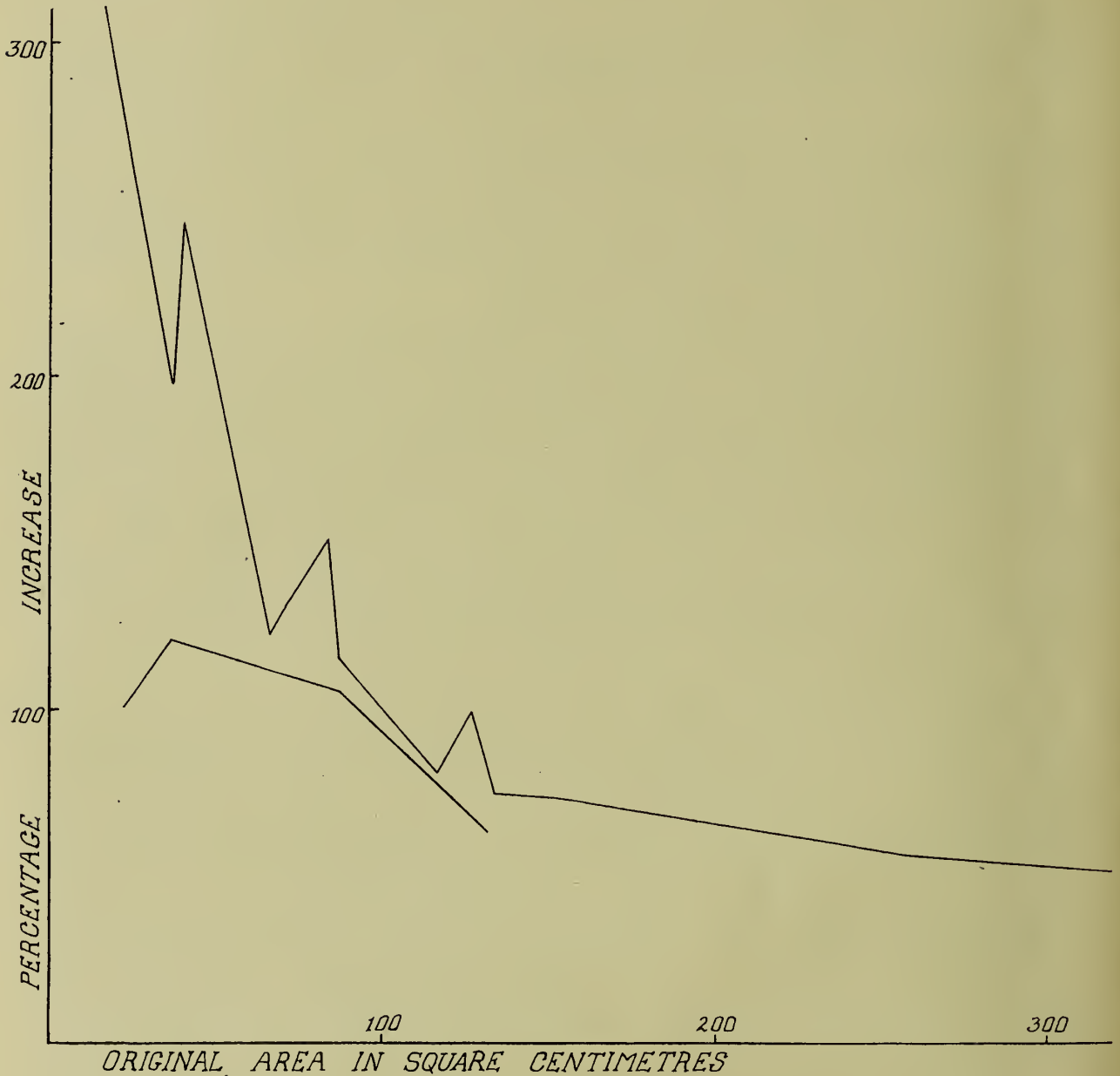
* The measurements made in connection with both the principal and subsidiary experiments are recorded in full in the tables at the end of the paper.

We have already seen that a difference in experimental period, of the order here involved, happens to have no significance for the interpretation of the results, beyond what has already been ascribed to it. At the same time it should be explained that the only reason why the period was not the same for all the corals was that in the case of experiments as laborious as those described, it is a physical impossibility to begin the experiment on a given day or even in a given week, unless a large number of persons are able to engage in it at once—a condition which could not be met on the present expedition. This will be readily appreciable to anyone who considers carefully the amount of manual work involved in the several stages of the method adopted; besides which the time available for such work on any one day or in any one month is limited by the tides (the anchorage pen being inaccessible except by diving, even at low water, on many days), and by sunshine (the corals can only be taken out of the water in the cooler part of the day). The one factor which is important is that the minimum experimental period should not be too short; and this condition was satisfied.

(2) ENVIRONMENT.—That a coral may grow very much more in a favourable environment than in a less favourable one is demonstrated clearly by cases such as the one illustrated in Plate VII, figs. 5–7. The two pens in which the experimental corals lived were subject to two different combinations of environmental conditions, one series more favourable to coral growth in general than the other. The growth of corals in the anchorage should therefore be considered separately from the growth of corals in the moat. On the other hand, this effect of environment should not be given too much weight. Its incidence is very different for different species of coral, and it applies chiefly to the more delicate forms which *normally live in the anchorage*, and which die or flourish less well in the moat. In the case of species which normally live in the moat, or which will live there fairly successfully, there appears to be little or no difference in the effects of the two environments upon growth.

(3) SIZE OF COLONY.—If a small colony and a large colony of the same species are taken, and are allowed to grow in the same environment and for the same length of time, one of them may grow proportionately much more than the other. In such a case the chances are that the small colony will grow more in proportion than the large one; but this is not necessarily the case, and the opposite may occur, particularly if the difference in size between the two colonies is not great. An example of the former occurrence is given in Plate I, figs. 3–6, and Plate II, figs. 1 and 2, in colonies of *Acropora squamosa*. The colonies illustrated in Plate I, figs. 5 and 6, and Plate II, figs. 1 and 2, were both kept in the anchorage, and the period of the experiment was 29 weeks and 2 days for both. The growth in the larger colony was 34% on each of two diameters, that in the smaller colony 106% and 105% on two diameters. The still smaller colony of Plate I, figs. 3 and 4, grew in the less favourable environment of the moat, and might therefore have been expected to grow less actively; and it was allowed to grow for 5 weeks longer than the others. With the last factor in its favour and the first against it, it achieved the enormous increase of 150% and 185% on two diameters; this difference is of such magnitude as to discount the effects of time and place, and is clearly correlated with the vigorous individual growth-power of the colony, which, though very small, grew far more in proportion than its larger counterparts in the anchorage. An example of the opposite state of affairs may be obtained from other colonies of this same species of *Acropora*. Colony No. 40a and Colony No. 57 were both healthy specimens of *A. squamosa*. Both were kept in the anchorage,

and the period of experiment was the same for both but for a difference of 4 days, which can have no significance. No. 57 was much larger than No. 40a, but it grew distinctly more strongly, its increase being 34% on each of two diametres, as against 29% and 26% in No. 40a.



TEXT-FIG. 2.—Graphs summarizing the data obtained by measuring the increase in area of 17 colonies of *Pocillopora bulbosa*. By "area" is meant the area covered by the coral; the comparison was effected by measuring the area of the projected image of the coral, before and after the experiment, on an enlarged photograph, with a planimeter. It will be noted that the increase for the smaller colonies is progressively greater than for the larger ones, and that all the specimens with an original area of less than 100 square centimetres have increased this area by 100% or more, up to the large increase of 310% in the youngest colony. The upper graph represents growth in normal colonies; the lower graph refers to half-colonies which were regenerating. For further comment, see p. 177.

Since variations of the nature just described are to be found in the amount of growth achieved in the same species, irrespective of environment, time, and size of colony, it is clear that if one attempts to construct a growth-curve for any species of coral, the individual points plotted will necessarily often lie wide of the curve itself. In the experiments here described, the number of colonies used for any single species was usually too small to enable us to construct a curve for it (nor was it our object to do this), but in one case, that of *Pocillopora bulbosa*, the data appear to lend themselves to this treatment fairly well. We wish to make it clear that, since the data presented for *Pocillopora* are few, we do not desire to base a final conclusion upon them: but they are so interesting and suggestive that we should like to put them on record in the hope that future workers will carry out further work on the same lines with much larger numbers. It may be pointed out, however, that even if a larger experiment involving hundreds of colonies were carried out, this would not eliminate the peaks and depressions which occur in the present graphs. These are due to normal individual variation and would always persist: but a large experiment might bring a majority of the points close to a definite curve. In the presentation of the lower graph in Text-fig. 2, specimens of the coral grown in moat and anchorage are treated together (the upper graph is based entirely upon moat-grown colonies): this is legitimate for the species in question, because it is one which both in nature and in the experiments grew well in both environments. If any conclusion may be drawn from Text-fig. 2, it is that in *Pocillopora bulbosa* the amount of growth falls off at a fairly definite but not constant rate as the colony grows larger; and that in specimens which have been divided and are regenerating the amount of growth is, for a time, considerably less than in normal specimens. It has been shown by Vaughan and Mayor also that as certain corals grow older their rate of growth declines.

(4) INDIVIDUAL VARIATION.—This factor is probably a potent one. Two corals belonging to the same species, growing in the same environment, for exactly the same length of time, can and do show striking differences in the amount of their growth, even though both are perfectly healthy and normal. We have already seen that such variation is sometimes correlated with differences in size, but also that it sometimes occurs irrespective of these. This variation means that the results of any experiment are bound to give very irregular figures, so that in summarizing the results in general terms it is preferable to use averages rather than to rely too much upon individual figures. As further examples of such variation we may take the following. In two colonies of *Acropora quelchi*, of approximately the same size and shape (10.85×10.13 cm. in the one case, and 11.20×9.96 cm. in the other), both growing in the anchorage, the increase in the first case was 57% and 78% on the two diameters, in the second 44% and 34%; this is a little further emphasized by the fact that the colony which grew the lesser amount had three weeks longer in which to do it. Again, in two colonies of massive *Porites*, measuring respectively 8.26×8.10 and 8.69×7.77 cm., both growing in the moat, the increase in the former case was 22% and 24%, in the latter 8% and 6%. In this instance there was a difference of two weeks in the experimental period, in favour of the colony which grew the most, but this can have had no more than a small effect on the result. The effects of individual variation in vigour of growth are not easily distinguished from those due to intermittent growth-rate; but in cases such as these, where the effect is considerable, it is probable that both factors are involved.

(5) THE FORM AND INTERNAL STRUCTURE OF A COLONY are obviously factors which

affect its rate of growth. A branched species may be expected to grow more rapidly than a massive one, and a species with slender branches more quickly than one with stout branches. Further, a coral of loose porous texture should grow more rapidly than one with a firm and dense skeleton. These expectations are, in general, confirmed by the results. They do not work out quite mechanically, but that again is to be expected..

CONCLUSIONS.—From the foregoing paragraphs, we may conclude that the most powerful of the factors which determine what the growth of a coral will be within a given period are the relation between its spells of active growth and spells of quiescence; its individual vigour or growth power; its shape, size and environment. The size factor will not be effective in every case; but it is evident that, apart from the factors of individual variation and spasmodic rate of increase, there is a distinct tendency for young corals to grow more rapidly than older ones. The next effective factor is that of environment; this will clearly determine where corals can establish themselves at all; but apart from this, it will affect some species much more than others. If a reef presents more



TEXT-FIG. 3.—Silhouettes of young colonies of *Montipora ramosa*, illustrating the growth that they made in 8 months. A and B represent the same colony at the beginning and end of the period; C represents a colony which started from a beginning which was probably even smaller than fig. A. All figures are to the same scale, about three-quarters natural size.

favourable and less favourable environments, certain species will be able to grow well in both, whereas others, if they can survive at all in the less favourable habitat, will grow but little there and will not reach a large size. There are intermediates between these two extremes. Lastly, the length of the given period will operate in this manner; if it is very short, the effect of the intermittent growth-rate may mask all others; if it is as much as several years, the effects of age and of average growth will become apparent; but if there is any question of a difference such as that between 6 and 9 months, this may have no effect, since it is quite possible for one coral to grow more in 6 months than another of the same species does in 9, for the reasons already stated. In connection with periods of several years, it should be remembered that corals reach limiting sizes at different ages, according to species, and that some of them probably normally live for a few years only.

In interpreting the figures presented in this paper all the factors just mentioned must be taken into account.

B. FURTHER CONSIDERATION OF THE RESULTS.

(1) THE COMPARATIVE GROWTH-RATES OF THE CORALS USED IN THE EXPERIMENT.—We have seen that it is advisable when considering the general results of a certain class

of experiment to use averages rather than individual figures. The averages presented are based upon perfectly healthy and normal colonies only, subnormal cases or specimens which died before the end of the experiment being omitted.

The average rates for a number of the colonies measured are summarized in the following table. It will be observed that the highest average increase recorded is that for *Montipora ramosa*, one of the commonest of the moat-dwelling species. If this average were based on a larger number of colonies (the casualties in this species were high, so reducing the number available for measurement), it would no doubt approach the average for *Acropora* more closely; but the astonishing rate of increase in the young colony of *M. ramosa* might even then raise the figure. This remarkable growth is illustrated in Text-fig. 3, which represents the history of two small colonies during a period of 31–32 weeks. In Figs. A and B we have silhouettes of a small colony at the beginning and end of the period, the increases on 3 diameters being 197, 206 and 237%. Fig. C is the silhouette of another young colony which sprang up from a beginning so small that it is not visible at all in the first photograph, being probably overhung by a large *Favia*. The original size of this colony is unknown, but at the end of the experiment it was larger than B, and apparently came from an even smaller beginning, so that the percentages here would be higher still.

Genus.	Average percentage increase in diameter. Based on the mean increase on two diameters.	Range of percentage increase in each genus.	Number of colonies upon which average is based.
<i>Montipora (ramosa)</i>	95	42–227	3
<i>Acropora</i>	57	13–185	35
<i>Pocillopora</i>	43	14–80	13
<i>Psammocora</i>	33	14–57	9
<i>Porites</i>	17	6–37	5
<i>Favia</i> and <i>Coeloria</i> *	10	3–22	17
<i>Lobophyllia</i>	10	$\frac{1}{2}$ –23	11
<i>Symphyllia</i>	10	1–29	6

* The species of *Favia* (with its subgenera) and *Coeloria* are treated together here, because the only species of *Coeloria* involved was *C. daedalea*, which, in the colonies used, was very little meandrine. The species grouped together all belong to one form as far as growth is concerned.

After *M. ramosa* comes *Acropora*, with an average of 57%; then the other branched forms, *Pocillopora* and *Psammocora*, with averages of 43% and 33%. The massive species of *Porites* form a link between the high rates (over 30%) of the branched corals and the low rates (10%) of the Astraeid genera *Favia*, *Coeloria*, *Lobophyllia* and *Symphyllia*. The position of *Porites* in this scale is interesting, in view of the fact that it forms a considerable percentage of the reef-substance in some of the reefs of the Great Barrier region. Its relatively rapid increase is probably connected with the fact that it is a perforate coral, whereas the Astraeids are imperforate.

(2) FURTHER DETAILS FOR CERTAIN GENERA.—*Acropora*.—The variety of growth-form in this genus is very great, as an inspection of the plates illustrating this paper will

make clear. Some of the extremes of form, however, are not found among the species used in the experiments—*e. g.* the largest types of stagshorn coral, the massive species such as *A. palifera*, and certain encrusting forms. Seven species (apart from a few small undetermined colonies) were used in Experiment I, and all of them proved to be rapid growers; but the actual rate naturally varied to some extent from one species to another, as well as from one colony to another within the same species.

We cannot give much information with regard to the relative *average* growth-rates of the seven species (although measurements of 43 colonies are given in our tables), because it was not possible to obtain, for the experiment, a reasonable number of colonies of every one of them; moreover, there were more colonies broken (by fish, etc.) during the experiment in some species than in others. Thus we were able to obtain measurements in the end from thirteen colonies of *Acropora squamosa*, and from fifteen colonies (including three varieties) of *A. quelchi*; but in the other cases the number was fewer, and in two species only a single colony survived. The average figures for each species, based on such numbers, could not be reliable. The conclusions stated in the next paragraph, however, probably represent the truth fairly closely.

Of the seven species used, one, *Acropora gemmifera* (Plate III, figs. 3 and 4), has as a rule more massive thumb-like branches than the others; this species appears to grow more slowly than the remaining ones. Which of the species grows most rapidly we cannot be certain; but two of them certainly grow very quickly indeed. Our only specimen of *Acropora hyacinthus* (Plate II, figs. 5 and 6), a young one, showed an increase of 99 and 127% on two diameters. This does not parallel the increase of 150 and 185% exhibited by a young specimen of *Acropora squamosa*; but in the case of *A. squamosa* (Plate I, figs. 3-6; Plate II, figs. 1 and 2) eleven normal colonies were available for measurement, and the average increase for these was only 54%. On the other hand, an average for *A. hyacinthus* would probably be higher than this, because it has more slender branches than most of the species used, and can probably grow quickly even when older. Another species which undoubtedly grows very fast is the stagshorn *A. pulchra* (Plate I, figs. 1 and 2), with branches of moderate thickness; here an average for four colonies gives an increase of 66%, and the performance of three of the four colonies measured was much greater than this. The remaining species are of intermediate standing. *Acropora squamosa*, and *A. quelchi* (Plate II, figs. 3 and 4) in its several varieties, have branches of intermediate degrees of thickness; these showed intermediate average amounts of growth, and would probably occupy an intermediate position on any computation. *Acropora exilis* (Plate III, figs. 5 and 6) did not increase strikingly in total diameter, in spite of its slender branches; but this is a species with more lateral subdivision of its branches than the other species measured, so that a good deal of its growth would be diverted into the lateral branches, and would not affect the total diameter of the colony. The single colony of *Acropora formosa*, a slender stagshorn, grew less than might be expected.

Montipora.—The rapidity of growth in the branching species *M. ramosa* has already been mentioned (p. 179). The type of increase which takes place in the foliose species is illustrated in Plate IV. The growth here is less rapid than in *M. ramosa*, but is nevertheless of considerable amount.

Seriatopora.—The single colony belonging to this genus increased 19 and 29% on two diameters. In this case the *upward* growth of the slender branches was probably greater than their lateral extension.

Astraeidae.—It has been seen already (p. 179) that the average amount of increase in *Favia* and *Coeloria*, *Lobophyllia* and *Symphyllia* is the same (10%). In addition to these, two colonies of *Galaxea musicalis* were measured. These gave an average increase of 10% also.

Fungida.—The results with specimens of *Fungia*, *Döderleinia* and *Herpetolitha* were distinctly curious. These forms do not lend themselves very well to attachment to a cement block, because the cement is bound to kill part of the flesh on the aboral side of the disc, and the attachment of a more or less flat coral to a flat block leaves it very much exposed. Notwithstanding this, the health of some of the specimens seemed to be excellent throughout the experiment. A specimen of *Fungia actiniformis* var. *crassitentaculata* was attached to a block in the anchorage pen. It was a large specimen, the skeleton measuring 17.5×18.5 cm. In this species the skeleton is as a rule invisible during life, being hidden under a mass of waving tentacles, the inner of which are some 6 in. in length. The expanded polyp is therefore much larger than the skeleton, and is a very conspicuous object. This coral suffered severely at first from contact with the cement; it changed from brown to nearly white; the tentacles became reduced, and the mouth gaped. The specimen appeared to be dying. Very shortly, however, it began to recover, and six weeks after it had been attached to the block it was thoroughly flourishing once more, with long brown tentacles and a closed mouth. It remained perfectly healthy until the end of the experiment, but did not increase in size by any measurable amount (the 0.4% increase quoted in the table on p. 212 is within the region of experimental error). Another specimen attached to a block in the anchorage, but belonging to a different species (*F. fungites*, one of the green and purple *Fungiae* whose tentacles expand only at night), suffered considerable retraction of its flesh at first, but also recovered completely in less than six weeks. This one also grew an inappreciable amount. Five specimens of another night-flowering variety which normally inhabits the moats were attached to blocks in the moat pen. None of these suffered any inconvenience from their attachment, but three of them died before the end of the experiment. The amounts of growth they exhibited, however, were very varied—from no appreciable increase (3% on one diameter and none on the other) in two cases to 10% and 13% on two diameters in another, the latter case being one in which the coral died 23 weeks after the beginning of the experiment. The specimens of *Döderleinia* and *Herpetolitha* were healthy throughout the experimental period, but increased by very small amounts (average increase 3%). Of the compound *Fungids*, *Psammocora* and *Pavona* were used. The results for *Psammocora* have already been noted (p. 179). Two portions of a large colony of *Pavona cactus* gave an average increase of 16%, and the development of one of these pieces is illustrated in Plate V, figs. 1–3.

Alcyonaria.—A few records of growth in the fleshy alcyonaria which form a considerable part of the population of the seaward slope of the reef are given in the table on p. 212. The three colonies measured give an average increase of 47%, and one of them is illustrated in Plate VI, figs. 5 and 6. One large colony of *Heliopora coerulea* was used. This colony probably died soon after the beginning of the experiment; but appeared to be in a state of suspended animation for a time, so that the exact time of its death could not be determined. In any case it grew only a very slight amount.

(4) A POSSIBLE DIFFERENTIAL GROWTH-RATE IN CORALS.—It will be shown farther on (p. 186) that when broken corals are regenerating, some of their branches may

regenerate much more rapidly than others. In some cases this inequality in regeneration appears to be quite irregular and directed towards no particular end; in other cases it appears that there is a fairly definite normal shape towards which the growth of the colony tends, and that if this normal shape is impaired by damage, branches will regenerate, or will grow out from neighbouring branches, to fill the gap, and will grow rapidly until the normal shape is restored. This is illustrated by the colony of *Pocillopora* described on p. 188, and represented in Text-fig. 4 and Plate VII, figs. 3 and 4.

It occurred to us that if so marked a difference in growth-rate may distinguish the individual branches of a regenerating coral, some less definite but still appreciable effect might be detected in the growth of a normal colony. An examination of the figures suggests that such an effect is demonstrable. In the following table some of the data obtained in Experiment 1 are summarized:

Genus.	Average percentage increase on greater diameter.	Average percentage increase on lesser diameter.	Number of colonies in which increase on greater diameter is greater than that on lesser diameter.	Number of colonies in which increase on greater diameter is equal to that on lesser diameter.	Number of colonies in which increase on greater diameter is less than that on lesser diameter.
<i>Montipora (ramosa)</i>	76	114	0	0	3
<i>Acropora</i>	52	62	14	1	20
<i>Pocillopora</i>	37	50	2	0	11
<i>Psammocora</i>	31	36	3	1	5
<i>Porites</i>	16	18	2	0	3
<i>Favia and Coeloria</i>	9	10	5	4	8
<i>Lobophyllia</i>	9	10	3	0	8
<i>Symphyllia</i>	8	11	1	0	5
Totals for the several genera			30	6	63

Total number of colonies to which the data refer, 99.

From the first two columns of the table the curious fact emerges that, in the 99 colonies to which these data refer, *the average percentage increase on the lesser of the two diameters measured exceeds the corresponding increase on the greater diameter in all the genera included in the table.* This suggests that if a coral is wider across one diameter than it is across another, it tends to grow more quickly where it is narrower; in other words it tends to grow in such a way as to cover a roughly circular area.* That this, if true, is a tendency and not an invariable rule, however, is shown equally clearly by the remaining columns in the table, from which it is evident that of the 99 colonies measured, 30 provided exceptions to the general tendency. Even then, a majority of 69 in 99 in favour of the existence of the tendency is fairly satisfactory, especially since some at least of the exceptions can probably be accounted for by special reasons operating in their particular cases.

A coral can naturally grow in such a way as to cover a circular area only if it has free space all round it so that it can extend in all directions. This condition is often absent in nature, since the coral may be prevented by rock, or by other corals, from extending

* We should say, from general observation on the reef, that such a tendency does exist. It does not, of course, apply in the case of corals of special shapes—e. g. *Herpetolitha*.

in given directions ; or may even be hemmed in all round. In the case of corals mounted on cement blocks, however, the colony usually has all the freedom required.

THE RESULTS OF SUBSIDIARY EXPERIMENTS.

Before describing these results we may point out that in Experiment 1 the number of coral colonies used (169) was large for a laborious experiment of this nature carried out by a few persons. In the case of the subsidiary experiments much smaller numbers had to suffice ; these experiments were side-lines for which we were able to spare a little time only. This is the only reason why larger numbers were not employed. The results, nevertheless, proved to be interesting.

EXPERIMENT II.

(*Transplantation of Corals to Different Environments.*)

Eleven colonies formed the material for this experiment. Each colony was divided as evenly as possible into two portions. The halves were attached to cement blocks as in Experiment I, and were planted out in the same two pens which were used for that experiment. One half of each colony was planted in the pen representing its original environment as a control ; the other half was planted in the contrasting environment. In other words, if the colony was collected in the moat, half of it was maintained there and the other half was transferred to the anchorage ; and *vice versa*.

The results of the experiment are recorded in tabular form on p. 213. It may be noted that none of the colonies appeared to suffer any harm from being divided into halves. Any disturbance caused by the operation was too slight to affect their health, even though it may have affected their rate of growth during regeneration.

Pocillopora bulbosa.—This species normally lives and flourishes in the moats. One would therefore expect that the halves kept in the moat would flourish, and that those planted in the anchorage (a locality more favourable to coral growth, to all appearance, than the moat) would do likewise. The four halves used in the experiment bore this out ; all survived and grew excellently.*

Montipora ramosa.—This again is a species which normally inhabits and flourishes in the moats. One colony was divided, and both halves achieved good growth. Whether the fact that the half kept in the anchorage grew more than the one in the moat has any significance, it is impossible to say on the basis of a single example.

Montipora.—A foliose species (Plate IV, figs. 1 and 2).—This was a colony belonging to one of the more delicate foliose species which, so far as we know, never occurs in the moat, where only certain coarser foliose forms are occasionally found. It is a typical open-water species, and our general experience suggested that it would not survive moat conditions. The result of the division of a single colony bore this out ; the half planted in the moat died very soon after transplantation ; the anchorage half flourished and grew well.

Acropora exilis and *Acropora formosa*.—These, again, are species characteristic of

* The great discrepancy between the increase on the greater and lesser diameters recorded in the case of No. A4 is apparently due to the fact that this colony was flat on one side, and that rapid growth on the lesser diameter took place, thus restoring the colony to reasonable symmetry. The case of this colony is dealt with in detail on p. 188.

open water, not normally found in the moat, and to all appearance of delicate constitution. One colony of each was divided. In both cases the halves kept in the anchorage flourished and grew strongly; and the halves kept in the moat died. In the case of *Acropora exilis* death occurred within a few days of transplantation; in that of *Acropora formosa* the colony died more slowly, and a single twig survived some time longer than the rest, but ultimately succumbed.

Acropora quelchi, var. 1.—This is a somewhat mysterious variety. It is a form of neat and characteristic appearance, common in the western moat, where it forms small colonies or small brackets. The branches are often blue-tipped. It has the appearance of being a young or stunted form of some species whose normal habitat is the seaward slope of the reef, and appears likely to be a modified form of *A. quelchi*. In the case of the single colony divided, the half kept in the anchorage grew well; that kept in the moat survived but made no progress.

Acropora squamosa.—This is a species characteristic of the anchorage, and attains normal stature only in open water. It is not uncommon, however, in the moat, but only in the form of young colonies; occasional larger colonies are to be found there, but always of subnormal size. A single colony was divided. Both halves survived, but the one kept in the anchorage grew much more strongly than the other.

Acropora hebes.—This is the only species of *Acropora* which normally flourishes thoroughly well in the moat (speaking of Low Isles only). Other species occur there, but usually only as young or exceptional colonies. It would therefore be expected that *A. hebes* would flourish both in moat and anchorage. Two colonies were divided. Unfortunately the moat-half died in one case, and the anchorage-half was broken by a large fish in the other (though it grew satisfactorily until broken). The two surviving halves, however—one in the moat and the other in the anchorage—both flourished and grew strongly. The growth achieved by the half kept in the moat is illustrated in Plate VII, figs. 1 and 2.

Acropora, species 1 (undetermined).—This species normally occurs in the anchorage, and only as young or struggling colonies in the moat. A very young colony from the moat was taken, and was divided. The remarkable result is illustrated in Plate VII, figs. 5–7, and is described on the page facing the plate. The result is a striking example of the way in which the growth of an organism may provide an index to the relative suitability of the two environments to the needs of a given species. It is true that one could not make any generalization from a single example, but the case is not the less suggestive on that account. The following data are direct measurements of the lengths of 10 branches in each of the two halves of this coral at the end of the experiment, and provide a means of comparing the growth of the two halves.

Lengths of individual branches in the half kept in the anchorage, measuring from base to tip.		Lengths of individual branches in the half kept in the moat, measuring from base to tip.	
70.4 mm.	80.75 mm.	30.5 mm.	33.0 mm.
80.0 "	80.95 "	31.25 "	34.5 "
80.0 "	90.05 "	32.55 "	36.0 "
80.55 "	90.25 "	32.75 "	36.5 "
80.7 "	90.95 "	32.85 "	38.25 "

CONCLUSIONS.—In an experiment dealing with 22 half-colonies only it is obviously not possible to generalize from the result, since it is always possible to maintain that the results may be due to accidents. On the other hand, in a case where general experience gained in the field leads to certain definite expectations, and in which these expectations are exactly fulfilled in 21 out of 22 cases (the single exception certainly *was* accidental), we have at least some reason to suppose that we are on right lines, and that the results of a larger experiment would bear out those of the small one. We think, therefore, that the following conclusions are probably justified:

(1) The species used which are normally inhabitants of the moat grow well both there and in the anchorage.

(2) The species used which are normally inhabitants of the anchorage either die in the moat, grow less well there, or fail to attain normal size.

EXPERIMENT III.

(*Regeneration of Branches in Colonies of Acropora.*)

This experiment was concerned with the marking of 30 colonies (all of them but one belonging to the genus *Acropora*), and its object was to obtain information relating to the rate of regeneration in branches belonging to this genus. The corals in this instance were not removed from their own habitat at all, but were marked *in situ* by one of us (T. A. S.) from a diving helmet. They were all situated in two small areas near the mouth of the anchorage, both places lying well below the level of low water of the lowest spring tides, so that the depth of water over the corals would never be less than some 8 or 10 ft. It was found that marking could be carried on for an hour and a half at a time below water, but that longer periods than this were unsuitable.

The method by which the corals were marked has already been described in the section on material and methods (p. 173). Of the 30 colonies marked, only 11 were recovered at the end of the experiment. This is due partly to the fact that the ones which had been marked with plasticene (p. 173) had not developed far enough to give a result; and partly to the fact that some of the colonies could not be re-discovered by the diver. This latter point will not surprise anyone who has worked below water, and who knows how short a distance before one it is possible to see, under submarine conditions. (It was not feasible under the circumstances to mark each colony with a buoy.)

When the material was recovered at the end of the experiment, sometimes the whole colony was brought up; in other cases only the branches which had been marked were collected. The measurements made are recorded in the table on p. 214.

In all the colonies recovered a number of branches had undergone regeneration of greater or lesser amount. The total number of branches which we were able to measure was 144. In all these cases the branches were broken cleanly across at various, but never very great, distances from their tips, so that the regeneration was always of a simple type.

The information obtained from the experiment is well illustrated by the figures on Plate VIII. In Fig 1 is shown the tip of a branch of *Acropora formosa*. This branch had

been broken off seven weeks before the condition reached in the figure was attained. The broken end was still almost flat, but the flesh had healed across it, and the axial polyp had regenerated a new distal end, and was surrounded by a ring of very small subsidiary polyps; the calices of these are visible as dots in the photograph. Figs. 2-5 (*Acropora polymorpha*) show further stages in the process. In the branch shown in fig. 2 the regenerated portion had become a short cone, surmounted by the now well-developed calyx of the terminal polyp, with numerous small subsidiary calices on its sides.* The branch illustrated in fig. 3 had formed a much longer cone of new skeletal material, and the lateral calices were well developed; but the site of the fracture was still conspicuous. In the next branch the situation of the fracture had become less obvious because the regenerated branch had become relatively stout; and one of the lateral polyps had become prominent and had started a new branch (on the right-hand side in the figure). In the last branch of the series (fig. 5) the regenerated part had become very well developed, and it occupies most of the figure. The point of fracture was by this time only just distinguishable, and the regenerated portion had become definitely trifid.

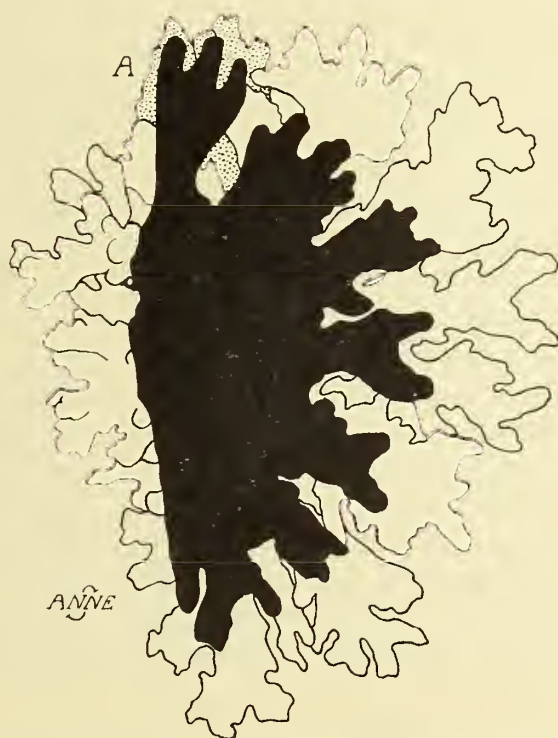
The general principle of the process of regeneration just described holds good for all the species of *Acropora* used in the experiment; but the details differ from one species to another. The new growth is always started by a regenerated terminal polyp, and is led by this polyp throughout. Lateral polyps appear on the sides of the regenerating cone, and when this cone subdivides into branchlets, each branchlet is headed by a terminal polyp which has been derived from one of the lateral ones. The differences of detail which supervene may be traced to the exact shape of the terminal calyx which is regenerated; to the form of the lateral calices; to the extent to which they project beyond the general surface of the branch; and to the form of that portion of the branch which lies below the fracture. Some of the varied appearances produced in the several species are illustrated in the later figures on Plate VIII. In figs. 6 (central branch) and 7 the new growth has the form of a narrow, chimney-like extension of the old branch; in fig. 8, which includes three regenerating tips, the broad shape of the new terminal calyx results in the production of a low rounded cone.

Apart from the details of the regenerative process, the experiment demonstrated a very curious fact, which again is illustrated by Plate VIII. All the branches shown in figs. 2-5 belonged to a single colony; they were all broken on the same day; and they all regenerated for the same length of time. Yet the amounts of regeneration attained by them were very different. Altogether thirteen branches were recovered from this particular colony, and the amount of regeneration varied among them from 4.0 mm. in the least active to 38.75 mm. in the most active, with all grades between (see table on p. 214). The amount of regeneration achieved by the most active branch, therefore, in the same time, was nearly ten times that achieved by the least active. The colony was perfectly healthy at the end of the experiment, and there was no indication that any of the branches were less healthy than others. On the contrary, our general experience with regenerating corals, throughout the year, would lead us to suppose that in many species such irregularity is perfectly normal and usual. This conclusion is supported by other

* In this figure there may also be seen a diagonal ridge on the part of the branch situated below the site of the fracture; this ridge was formed by an overgrowth of the tissue and skeleton of the coral round the silver wire which marked the branch. The wire was completely embedded in the part shown. This is a frequent occurrence in marked corals.

colonies in this particular experiment, and similar results have been recorded from Cocos-Keeling Islands by Wood-Jones, who also describes the dominance of the terminal polyp in regeneration, and the variations in the development of a branch which may occur according to whether or not the terminal polyp is prevented, by the nature of an injury, from regenerating ('Coral and Atolls,' 1910, pp. 69, 82, 111, etc.).

Is there any connection between irregularity of regeneration and the general growth-form of the colony? We cannot answer this definitely from the experiment, but we think that it might be possible to demonstrate such a connection. In the case cited above (*Acropora polymorpha*) the colony was one of straggling stagshorn growth, with no particular general form, such as would naturally be produced by irregularities either of regeneration or of ordinary growth. There are other species, however (for instance *A. squamosa*, Plate I, fig. 6), in which the adult colony forms a dish-like or shelf-like structure



TEXT-FIG. 4.—Diagram illustrating the change of form which took place in a small colony of *Pocillopora* during a period of 31 weeks. The details are described on p. 188. The shape of the colony at the beginning of the experiment is indicated in solid black; its shape at the end, in outline. The branch A (stippled) died after making the amount of growth shown. The diagram is slightly larger than natural size.

with a stem underneath or at one side. In such a case the branches which spring from the upper surface of the expansion tend to be neatly arranged, and their tips attain a fairly even common level; and it might be expected that during regeneration they would grow new tips at a fairly even rate. Unfortunately our results include no clear case of this description; but the nearest approach to it is shown by colonies 4 and 5. These were colonies of *Acropora gemmifera* (Plate IX, fig. 1), in which there was some approach to a general surface-level in the tips of the branches (though less definitely than in *A. squamosa*);

and here the amounts of regeneration shown were more regular than in *Acropora polymorpha*, though even here the maximum new growth was two or three times the minimum (but this is much less than ten times). *Acropora formosa* is one of the stagshorn species, and the irregularity which it exhibits is therefore in order. In *Acropora quelchi* the results should be fairly regular, whereas the measurements made reveal considerable irregularity. This is more apparent on paper than in fact (all the amounts being small); in a colony which was collected entire (No. 6), the regenerating branches had their tips at a fairly even level, much as in the photograph of *A. gemmifera* on Plate IX, fig. 1.

Before leaving the question of regeneration we may add certain data on the subject which may be gleaned from Experiments I and II.

In Experiment I, No. 40b, *Acropora quelchi*, a compound branch was accidentally broken off near its base, at the beginning of the experiment. Twelve weeks afterwards this branch had regenerated about half an inch; by the end of the experiment (30 weeks after the breakage) it was not certainly distinguishable from the other branches, and its total growth could therefore not be accurately determined. Whatever its exact growth, however, this branch and the neighbouring ones between them had filled in the gap in the outline of the colony left by the breakage, and had restored its proper symmetry.

In Experiment II, No. A4, *Pocillopora bulbosa*, the original colony had been halved so neatly that one of the halves (A4) was almost flat on one side. By the end of the experiment new branches had appeared on the flat side, and had become very well formed, so that the shape of the whole colony had become normal once more. This colony is illustrated in Plate VII, figs. 3 and 4, and also in Text-fig. 4. The text-figure was constructed by superimposing tracings made from the photographs taken at the beginning and end of the experiment; it was possible to do this accurately by reference to fixed marks which were the same in both photographs. From this figure it may be seen (1) that the branches on the uninjured side have continued to grow actively; (2) that the branch labelled "A" died after making a little growth; and (3) that a series of new branches has been formed on the broken side. Unfortunately the latter branches were foreshortened in the photograph, whereas the normal branches were recorded more in profile, so that the amount of growth in the new branches is minimized in the text-figure; but it may be seen from the plate that their growth was of considerable amount.

EXPERIMENT IV.

(*The Growth of Corals Derived from Planulae which settled on Material Planted Out on the Reef.*)

One of our earliest activities on the reef was to fix in various places on its surface collections of clean material, upon which we hoped that coral planulae would settle. The materials used were logs of wood, pieces of clean beach-sandstone which had not been attacked by organisms, short lengths of earthenware drainpipe, glass jars fixed in wooden crates and the cleaned shells of clams. These objects were fastened down by means of several devices, so that they could not shift, and were placed in a variety of habitats. In this experiment the date on which the materials were fastened down is known, and also the date upon which young corals were collected from them; but the dates

upon which planulae actually settled are, of course, unknown, so that the age of any young colony can only be stated as something not exceeding, and usually *less than*, the period of the experiment.

The variety of animals which attached themselves to these materials was not very great. The materials were left untouched, for the most part, for nearly eleven months; during this time a good deal of fine sediment was deposited upon and among them, and this appeared to interfere somewhat with their colonization by animals. The algal succession was interesting, more especially during the first few weeks, when a growth of microphytic forms sprang up on the surface of most of the materials.* Later on some of the materials became clothed by a strong growth of *Padina*. We feared that the early coating of algae and sediment might prevent any corals from settling at all; but by the end of the experiment about 40 young colonies had become established. Thirty-six of these were collected without damage, and their sizes, at the end of the experiment, are recorded in the Table on p. 215.

Of the 36 colonies recovered, 26 belong to the common moat-dwelling species *Pocillopora bulbosa*. This coral seems to establish itself under such circumstances more readily than any other. This is borne out by the fact that if one wishes to obtain a series of very young colonies the best places to visit are the "gaps" (actually regions of low level, not actual interruptions) in the rampart, through which water streams out after the sea itself has deserted the flat, on the ebb tide; and through which it streams once more, on the flow, before the whole flat is inundated. In one of these gaps, in 1929, a large number of young Pocilloporae had managed to establish themselves, the planulae presumably being left behind by the streaming water in angular crevices of the shingle. Young colonies of *Acropora* were also frequent here, but *Pocillopora* predominated.

The young Pocilloporae which had grown on our clean materials were of very different sizes, no doubt partly because they had settled at various times throughout the 11-month period. The largest colonies had formed well-developed small sheets of polyps, with diameters such as 11.0×10.0 mm., 10.4×7.7 mm., and 14.5×9.5 mm. In 14 of them the first vertical branch had appeared. In some of these the branch is still in an incipient condition, forming simply a hump on the basal expansion. In the more advanced specimens it has become a definite branch, and in one of them (No. 14) it has become trifid at the tip.

Apart from the Pocilloporae, we obtained 7 colonies of *Porites*, 1 of *Cyphastrea*, and 2 of an undetermined coral, perhaps also a Poritid. The largest colonies of *Porites* were 7.0×6.0 mm. and 12.0×6.5 mm., and this size they attained in twenty-seven weeks.

The experiment therefore established the following points:

(1) *Pocillopora bulbosa* will settle readily in the moats at Low Isles, and may form an expansion measuring as much as 11.0×10.0 or 14.5×9.5 mm. in less than eleven months. It may also form a trifid branch during this period.

(2) *Porites* may attain sizes such as 7.0×6.0 or 12.0×6.5 mm. in twenty-seven weeks or less, in the Low Isles moats.

Certain other animals settled on the materials, as well as corals, and the largest of these were also measured at the end of the experiment. In a box of materials planted in the anchorage there were found two colonies of the interesting polyzoan *Retepora graeffei*,

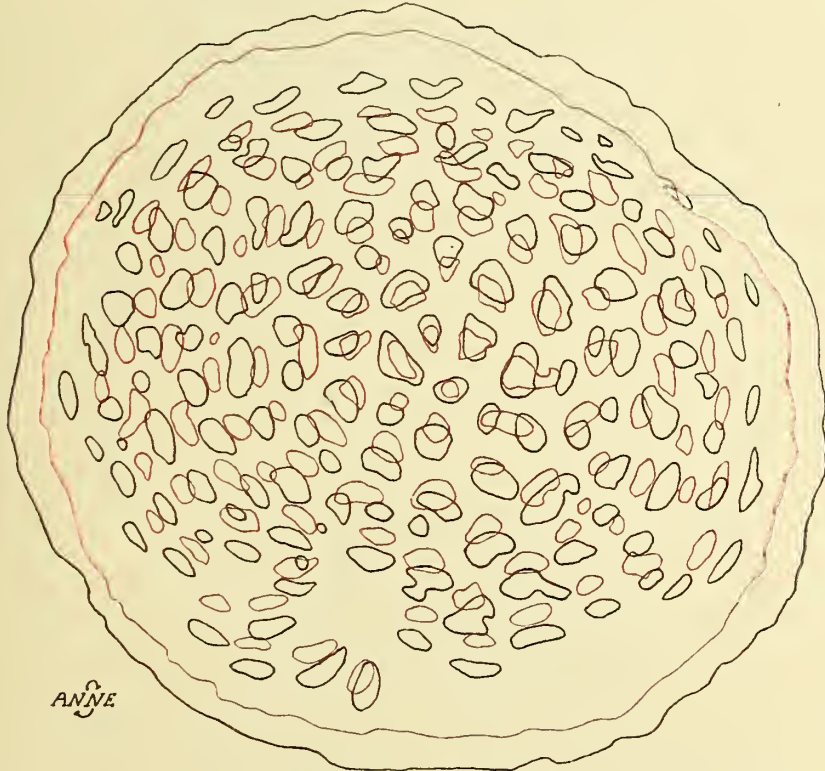
* Some details of the algal succession will be provided by G. Tandy in the systematic report on the algae.

which had attained heights of 21.0 mm. and 13.0 mm. respectively (forty-three weeks or less). An organism which grows very rapidly in the moats is the sponge *Gellius fibulatus*, with which is combined an alga. The organism forms straggling green branches, which may attain lengths of 100 mm., 105 mm., etc., in a period of sixteen weeks. Oysters of several species also settled on the materials, and the sizes of these are recorded on p. 215. Vermetids had also settled, and attained diameters up to 12.8 mm. during the experiment.

BUDDING IN ASTRAEID CORALS.

The question of asexual reproduction among the Madreporaria is one of considerable interest. It is a question about which much has been written, but about which the sum of our actual knowledge is still quite limited. In the early days two processes (budding and fission) were assumed to take place from a study of the skeleton; and even when a study of the soft parts was undertaken, notably by Duerden, the idea of the prevalence of these two processes remained. Duerden, in his monograph on the West Indian Madreporarian polyps (1902, p. 497), remarks: "Although the stages in division of the mouth or stomodæum have not been actually observed, the results to be detailed below prove conclusively that in fission the stomodæal wall is actually divided into two equal or unequal parts," etc. In spite of this conclusion, the tendency of recent work has been all in the other direction. Matthai, in his paper on asexual reproduction in the Astreaeidae (1926), claims quite fairly that in the species which he studied the process of stomodæal fission does not exist at all; and further, that there is as yet no evidence of its occurrence in any Madreporaria. Matthai therefore substitutes for "fission" and "budding" a distinction between two varieties of budding, (a) *extra-tentacular budding*, in which a new polyp appears from tissue lying outside the tentacular crown of any existing polyp; and (b) *intra-tentacular budding*, in which a new mouth arises on the peristome of an existing polyp, inside its circlet of tentacles, in correlation with an extension of the peripheral part of this polyp; followed in some cases by a gradual separation of the new part from the old. More polyps than one may arise simultaneously in this way. This process is the "fission" of earlier authors, but it involves in fact the creation *de novo* of a mouth and throat from tissue belonging to or lying below the peristome, without any subdivision of an existing mouth or stomodæum; preceded and accompanied by gradual extension and modification of form in the surrounding parts, but not by any process of rupture. Matthai's conclusions, like Duerden's, are based primarily upon a study of serial sections; neither author has seen the processes described take place in the living animal. In spite of this, Matthai has, to our way of thinking, demonstrated his case for the Astreaeids; and we hoped whilst in Australia to supply observation of living polyps which would confirm his work. It proved impracticable, in view of precedence of other work, to observe any given colony continuously, except in the cases of young *Pocillopora* and *Porites* (neither of them Astreaeids), in which the method of extra-tentacular budding was observed in detail and has already been described (Vol. III, No. 3 of these reports); but a few data referring to Astreaeids in which intra-tentacular budding takes place were also obtained, and these are presented here. Although they do not include direct observation of the *de novo* formation of new mouths, they do include the record of a formation of new mouths which can hardly have taken place in any other way. They fall into line very well with

Matthai's conclusions; and we saw nothing at any time which would suggest that subdivision of an existing mouth or throat ever occurs. In this respect the Madreporaria contrast with the Actinians, in which fission of a sudden description, involving rupture of both body-wall and stomodaeum, has been fully observed in living animals (Stephenson, 1929). Matthai's statements must also be modified to this extent—that fission, including subdivision of the throat, has been directly observed by Evans in *Corynactis*, which, according to our view of Anthozoan relationships, must be classified, not as an anemone, but as an aberrant madreporarian which produces no skeleton.



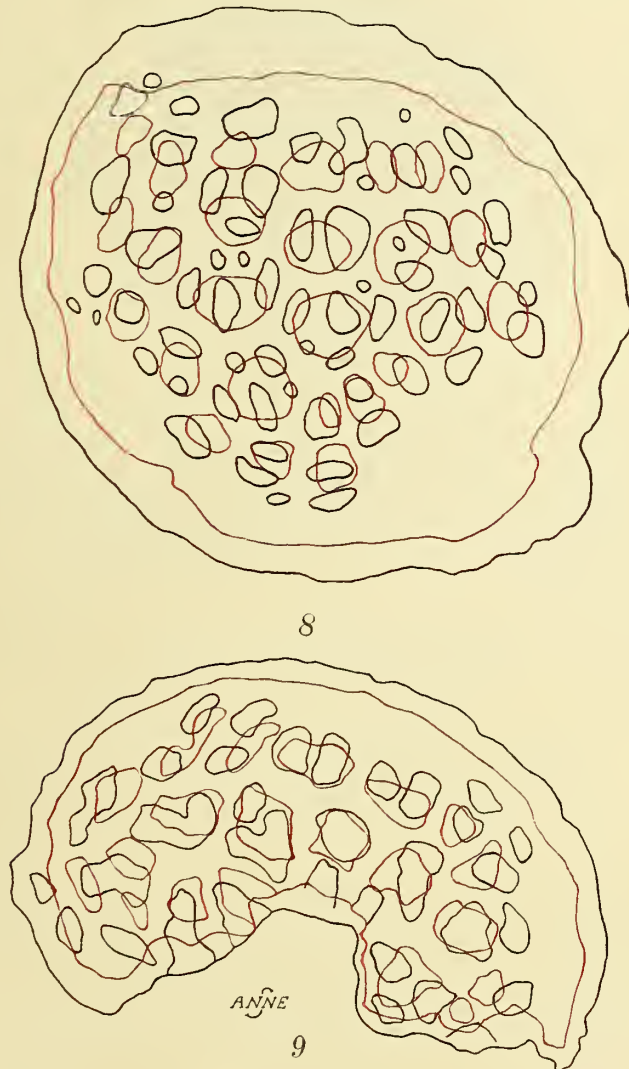
TEXT-FIG. 5.—Increase of polyps in *Favia*; no. 70. See text, p. 191. The red lines indicate the outline of the whole colony, and also the outlines of the calices of individual polyps, at the beginning of the experiment; the black lines indicate the same features some months later. In the centre of the figure the new and old outlines of the polyps are more or less coincident; as the edges are approached the new outline becomes more and more peripheral to the old one.

SUBDIVISION OF POLYPS IN *FAVIA*.—A number of the colonies used in Experiment I belonged to the genus *Favia*. In several of these the photographs taken at the beginning and end of the experiment showed clearly what had happened to individual polyps in the interval. One of these pairs of photographs is reproduced on Plate VI, figs. 1 and 2, from which the clarity of the evidence produced may be seen. In the case of five colonies the changes were worked out in detail, and are summarized in the following table: and to these are added details of a sixth small colony on which observations were made direct. In making the counts from photographs only the polyps in the central parts of each colony were used, since those round the edges were represented at angles which made them unsuitable for observation.



TEXT-FIGS. 6 AND 7.—Increase of polyps in *Favia*; nos. 80a (above) and 48b. See text, p. 191.
Conventions as in Text-fig. 5.

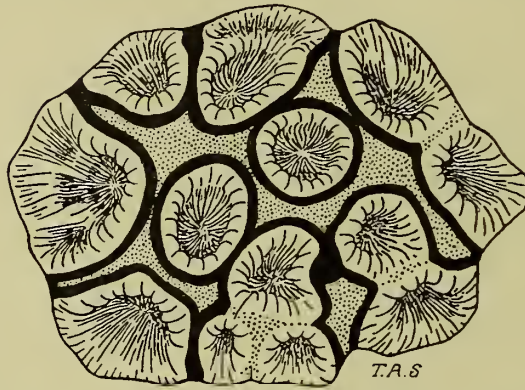
The changes which took place in the colonies in question are represented graphically in Text-figs 5 to 10. From the table it will be evident that the 259 polyps counted at the beginning of the experiment had become 394 by the end of it; that of the original 259, more than half were still undivided at the end, though many of these had altered in shape



TEXT-FIGS. 8 AND 9.—Increase of polyps in *Favia*; nos. 81b (above) and 2a. See text, p. 191.
Conventions as in Text-fig. 5.

as one of the preliminaries to subdivision; that of the remainder, a high majority had divided into two, a considerable number into three, and a very few (six only) into more than three, the maximum being reached in the case of a single polyp which became transformed into six new ones. (In the wording of the last sentence, as in the table, it is assumed that the process of multiplication of polyps was one of intra-tentacular budding in every case; it is possible that in a certain proportion of cases new polyps had arisen by the extra-tentacular method; but if so these would be quite in a minority.) We do not wish to express any opinion as to the details of the process by which these new polyps arose

(a matter dealt with fully by Matthai), but would point out that in the cases where more than three polyps were present at the end of the experiment, in the space previously occupied by one, these may have been produced by abnormal means, or by successive processes; they need not necessarily have arisen by a single multiple subdivision.



TEXT-FIG. 10.—Increase of polyps in *Favia*; no. 92a. This figure represents diagrammatically the appearance of a young colony at the end of the experiment, but the recent developments which have taken place in the several polyps are indicated by thick black lines. Each polyp, or group of 2 to 3 polyps, enclosed in a black line, was represented by a single polyp at the beginning of the experiment. Of the 9 original polyps, 4 have become definitely subdivided, and one of the remaining 5 is well on the way to becoming three. The coenosarc between the contracted polyps is stippled. About twice natural size.

Increase of Polyps in Favia.

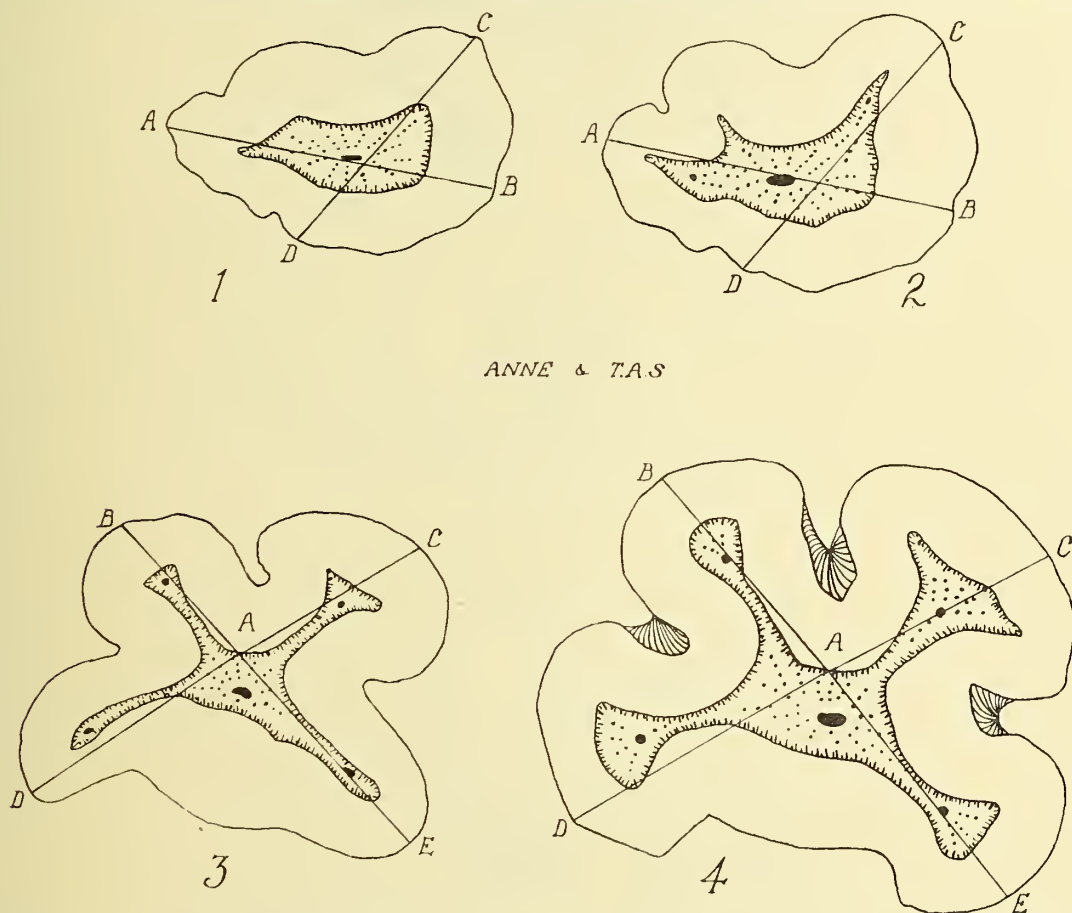
Reference No.	Name of coral.	Period of experiment.		Number of polyps examined	Number which remained undivided.	Number which became 2.	Number which became 3.	Number which became 4.	Number which became 5.	Number which became 6.
		Weeks.	Days.							
48b	<i>Favia doreyensis</i>	33	0	50	34	12	3	1		
80a	" "	31	2	41	16	19	5	1		
70	" "	33	1	114	91	21	2			
2a	" <i>favus</i>	31	1	20	7	12	1			
81b	" <i>doreyensis</i>	31	2	25	5	10	6	1	2	1
92a	" sp.	26	5	9	5	3	1			
Totals for the six colonies . . .				259	158	77	18	3	2	1

It may be noted that the increase in the number of polyps, in a period of about eight months or less, was surprisingly great, considering the massive nature of the colonies and their relatively slow rate of growth. In these *Faviae*, however, the history of the mouths could not be followed.

SUBDIVISION OF POLYPS IN LOBOPHYLLIA.—In several of the colonies of *Lobophyllia* used for Experiment I, detailed maps and measurements of the colonies were made at the beginning of the experiment, in the hope that the development of each colony might be followed out. Six of these colonies survived the experiment, and were again mapped

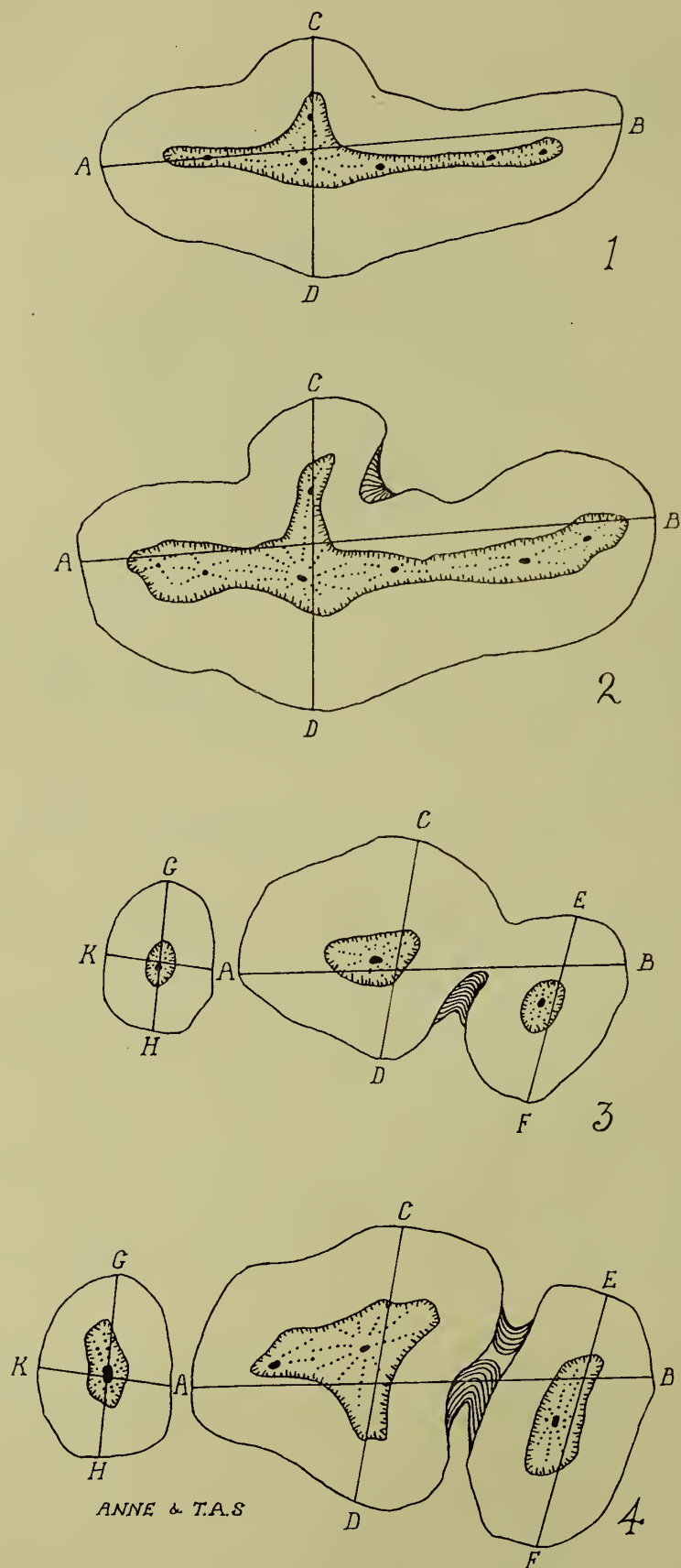
and measured afterwards. These colonies provided the details summarized in the following table, and represented in Text-figs. 11–14.

In the case of these *Lobophyllia* the change which took place in the colonies during a period of about seven months was less marked than in the case of *Favia*. This is to be

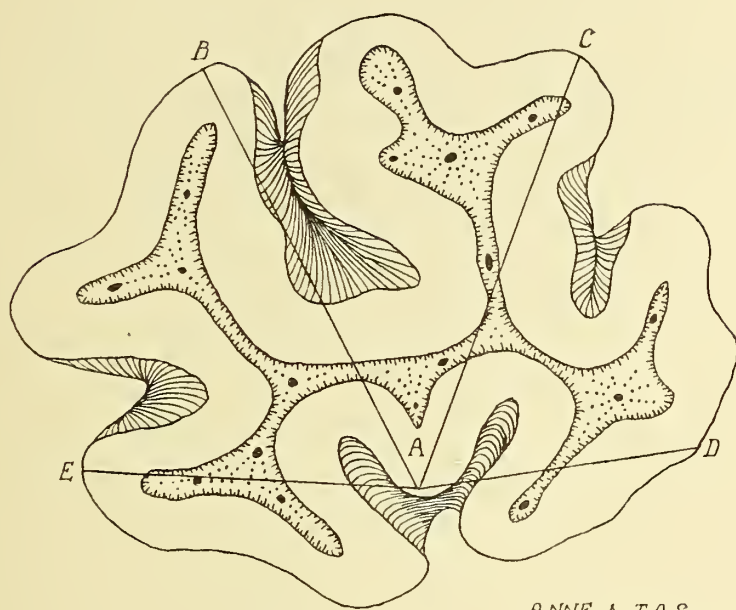


TEXT-FIG. 11.—Development of polyps in *Lobophyllia*. The lengths of the diameters indicated by straight lines are given in the table on p. 199. The figures are purely diagrammatic, but are drawn to scale, so that the increase in size as well as the development in shape is represented; but the corals are curved, and have to be represented in the diagrams as flat. Figs. 1 and 2 represent the same coral (no. 54a) before and after the experiment; Figs 3 and 4 represent another coral (no. 53a) in the same way. The mouths are black, the peristomes stippled; the line surrounding each peristome represents the margin of the column wall, drawn in over the retracted tentacles; the upper part of the column wall, which covers the outer parts of the septa, is unshaded; and the outer wall of the colony, covered by the tissues of the edge-zone (where visible), is shaded with lines. The changes represented in this and the succeeding figures are described on pp. 194–9.

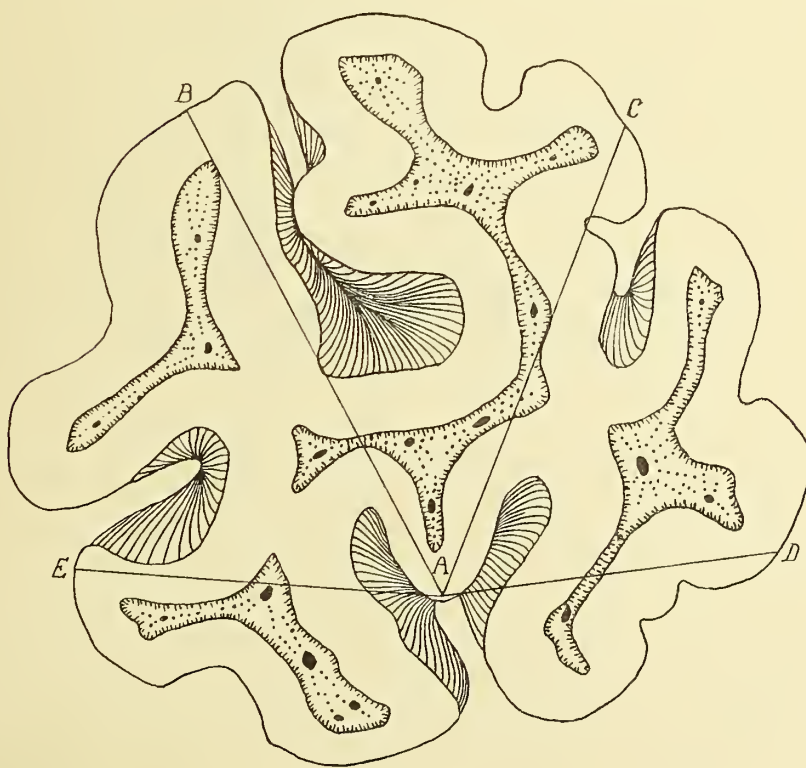
expected, since the polyps of *Lobophyllia* are very much larger than those of *Favia*, and are also more or less meandrine—that is to say, do not so readily subdivide. The actual number of polyps only increased from 12 to 16 in the time; but apart from this there was an appreciable extension and development of the sinuous shapes of the polyps, in all the colonies, as may be seen from the text-figures. In addition to this, the polyps studied started by having forty-seven mouths among them, and ended up with fifty-nine, *i. e.* twelve new mouths had come into being during the experiment. Now it is true that the



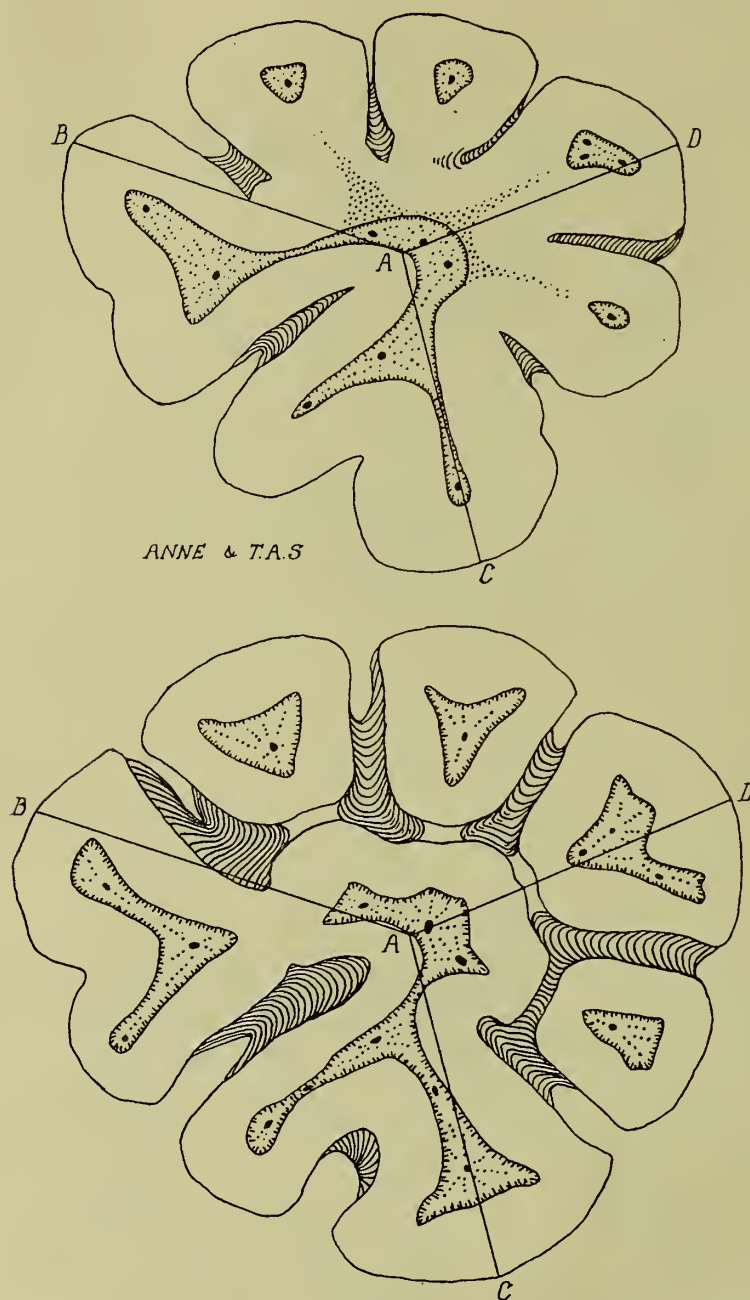
TEXT-FIG. 12.—Development in polyps of *Lobophyllia*. 1 and 2, no. 92e before and after the experiment; 3 and 4, no. 92d, before and after the experiment. Conventions as in Text-fig. 11.



ANNE & T.A.S



TEXT-FIG. 13.—Development in polyps of *Lobophyllia*. No. 53b before and after the experiment. Conventions as in Text-fig. 11.



TEXT-FIG. 14.—Development in polyps of *Lobophyllia*. No. 54b before and after the experiment. Conventions as in Text-fig. 11, except that in the upper figure there is some close stippling on the upper part of the column wall, indicating the remains of an earlier stage of development. The peristomes of the three polyps with which this stippling is connected have become distinct from the principal peristome of the colony, but their peripheral tissues are still in continuity with those of the large polyp. In the lower figure the smaller polyps have become distinct, but in three of them a little bridge of edge-zone, left white in the figure, still links them slightly to their parents. In the smallest polyp even this bridge has been lost.

Development in Polyps of Lobophyllia.

Reference No.	Period of experiment.		Measurements in centimetres.		Number of polyps at beginning of experiment.	Number of polyps at end of experiment.	Number of mouths at beginning of experiment.	Number of mouths at end of experiment.
	Weeks.	Days.	Original measurements.	Increase.				
53a	29	5	AB 2.3	1.0	1	1	5	5
			AC 2.7	0.5				
			AD 3.25	0.7				
			AE 3.32	0.48				
53b	29	5	AB 6.22	0.94	1	4	17	23
			AC 6.07	0.53				
			AD 3.74	0.75				
			AE 4.39	0.43				
54a	29	5	AB 4.35	0.28	1	1	1	3
			CD 3.55	0.44				
54b	29	5	AB 4.5	0.62	5	6	15	17
			AC 4.15	0.45				
			AD 3.9	0.65				
92d	26	5	AB 5.54	1.04	3	3	3	4
			CD 3.16	0.78				
			EF 2.72	1.0				
			GH 2.15	0.44				
			KA 1.52	0.4				
92e	26	5	AB 7.46	0.74	1	1	6	7
			CD 3.42	0.98				
Totals	12	16	47	59

All six specimens came from and were kept in the Anchorage. Nos. 92d and 92e were pieces from large colonies; the remainder were complete young colonies. The distances measured on the colonies are indicated in Text-figs. 11-14. More than one species is represented, but identification of young colonies is very difficult.

actual birth of these new mouths was not witnessed by anyone; but some of them were situated, at the end of the experiment, in places which they could not have reached without having actually moved a considerable distance across the peristome, if they were derived by fission from pre-existing mouths. There seems to us to be no doubt that they arose *de novo* and *in situ*, and that migration from the site of another mouth is out of the question. This is particularly well brought out by Text-fig. 11, figs. 1 and 2, in which the polyp began with one mouth and ended with three; and the two new ones are situated at distances of 9.0 and 13.5 mm. respectively from the old one. If these new mouths had arisen from the single original mouth, they would have had to migrate across distances of *pre-existing* peristome comparable to their distances from the old mouth at the end of the experiment; but, although the interval between two adjacent mouths can and does increase as the polyp grows (by interstitial growth of the intervening tissue), there is no reason to suppose that the newly-formed mouths, in a case such as this, have performed, across tissue already in existence, a migration of the magnitude demanded by the supposition that they arose from the original central mouth. The distances which separate new mouths from old ones in the other colonies studied also support this conclusion.

THE RELATION BETWEEN FORM AND ENVIRONMENT IN CORALS.

By T. A. STEPHENSON.

Among the discussions which have been written on this subject, one of the most notable is that of F. Wood-Jones, in 'Coral and Atolls' (1910)*. Before proceeding to Australia some of us read this account with great interest, and it fell in so well with our expectations and appeared so soundly based, that we were inclined to take it for granted that our work would tend to confirm the author's views. As the year progressed, however, we found that some modification of these views seemed necessary; but although we are obliged to dissent in certain respects from the well-known views expressed in 'Coral and Atolls,' we should like to acknowledge the stimulus which we received from that most valuable work. Our object in criticizing Wood-Jones's conclusions is not destructive, but aims at advancing our knowledge of the problem of species among corals by modifying a theory which, though undoubtedly true in its broad outlines, is probably mistaken in its detailed applications.

The gist of Wood-Jones's argument, if I understand it rightly (and many of his statements are so definite that there seems to be little room for misunderstanding), is that there are in reality far fewer species of coral than the systematic literature would lead one to suppose†; and that the effects of environment are paramount in determining the shape, and even the details of texture, which a colony will assume.

Now up to a point I agree with this entirely. The identification of an isolated colony or fragment of coral, the circumstances of whose life are unknown, by anyone who is unfamiliar with the reef from which it came, is sometimes quite possible; but in many cases it is so difficult that it may, without exaggeration, be described as an impossibility. The result of this has undoubtedly been the creation by systematic workers of many "species" which would be found, if they could be studied more fully, to be nothing more than growth-forms of one another. I also admit freely—and the fact is very important—that environment influences growth-form in corals.

On the other hand, I feel equally definitely that Wood-Jones has represented his case a good deal too strongly, and that he has exaggerated the influence of environment very much; and that, although he is right in thinking that there are fewer coral species than the literature would lead us to suppose, he nevertheless very much underrates their number.

Even though there may, in fact, be nothing more than a difference of degree between our views and those of Wood-Jones, I suspect that the effect of his work, together with the general difficulties of coral systematics, has been to leave in the minds of a number of people the question: "Are there species among corals at all?" Since this question is one of very considerable interest, and one which, if solved, will advance our knowledge of natural processes very greatly, I feel that a discussion of Wood-Jones's views in the light of new evidence is justified. Before commenting on them in any detail, therefore, I will

* First issued in 1910, re-issued in 1912.

† That some of our most experienced systematic workers would agree with this opinion is evidenced by such remarks as the following (Vaughan, 1918, p. 161): "It is not practicable here to review the species of *Acropora* reported from the Great Barrier Reef, as such a task is probably not possible without a critical study of Brook's types and of the other specimens examined by him. However, I will say that I doubt if half as many species as he recognized will be found valid."

present a short account of the distribution of forms of growth upon Yonge Reef, a reef belonging to the Outer Barrier series which is exposed to strong surf from the open Pacific.

With Wood-Jones's views in mind I asked Dr. E. A. Fraser, during our visits to the reef, if she would examine the distribution of corals upon it with the express purpose of finding out whether their distribution accorded with the ideas of Wood-Jones; if she would also collect a series of specimens illustrating her conclusions. The resulting notes and collections made it possible for me to write the following paragraphs with some backing for my view, and I am much indebted to Dr. Fraser for the assistance thus provided. I myself kept this investigation in mind when examining the reef, and came to the same conclusion as Dr. Fraser; and a summary of the notes, to which we both agreed, was written at the time. The result of these observations may be expressed as follows (the terms used in connection with Yonge Reef may be understood by reference to Vol. III, No. 2 of these reports, in which the reef is described):

Collections of corals were made, and notes were taken, in each of the four zones of the reef which lie nearest to the position occupied by the breakers at low water of low spring tides,* these zones being successively (starting at the edge of the reef nearest the breakers) the outer ridge, the outer moat, the reef crest and the inner moat. On the outer ridge one stands a few yards only from the point at which the waves actually curl over and break; and the ridge is even then constantly washed by the surge of the waves beyond their breaking-point. The outer moat is also much swept by this surge. The reef-crest rises entirely above the sea at low spring tides, but has pools on its surface; and the inner moat forms a series of pools, which at such times are relatively quiet.

In the first place the growth of coral at and near the seaward edge of the reef is often rich and varied. This is apparently in contrast to the state of affairs on some atolls, among which is Cocos Atoll. "In that area on which the surf beats—the seaward edge of the barrier—living coral growth reaches its minimum of individuals as well as of species" ('Coral and Atolls,' p. 159).

Secondly, on the outer ridge and in the outer moat many of the colonies of *Acropora* have short stumpy branches, and forms with very solid conical branches are common; but there exist in addition many large bracket-like growths made up of delicate branches. It is true that the basal parts of the branches are very stout and anastomosing, and the terminal branches short; but the latter are very easily broken. Further, one of the most delicate of all the species of *Acropora*, *A. delicatula*, occurs in this wave-swept region, and is common, among other places, on the sides of fissures in the outer ridge; and this coral is so breakable that it is very difficult to collect an intact specimen of it, the least tap with a chisel being enough to break any of its branches. On the contrary, large or straggling stagshorn corals naturally do not occur in the wave-zone, since they would be torn up; though a heavy stagshorn with creeping branches (*A. decipiens*) is common.

On the reef crest the selection of species is somewhat modified, probably partly by the fact that many of the colonies which grow there are fully exposed at low water of low spring tides. Common forms here are strong tuft-like colonies of *Acropora gemmifera* (with short stout branches) and *A. squamosa*; but the breakable stagshorns *A. hebes*

* This account of Yonge Reef describes only the state of affairs which prevails at low water of low spring tides, since we were unable to visit the Reef at other times. In writing the discussion, however, allowance has been made for the fact that the conditions vary with the rise and fall of the tide.

and *A. pulchra* also occur. This reef crest is decidedly bare in some places, but quite well populated in others.

In the inner moat all the main growth-forms mentioned for the outer ridge and moat are also to be found. It is not until the "anchorage coral zone" is reached that any profuse growth of straggling forms is present; and by this time we are definitely on the leeward side of the reef. But even here there is the somewhat contradictory feature that forms of *Acropora gemmifera* with distinctly short, solid, conical branches are common on coral heads to leeward of the reef, half a mile or more from the low-water position of the breakers.

This means, then, that apart from tall stagshorns, any of the principal growth-forms of *Acropora* may be characteristic both of the outer ridge and of the regions behind it. This statement need only be qualified to this extent—that on the outer ridge the stumpiest forms are probably at their most plentiful, and are often present in their most exaggerated degree.

I feel that the account just given does not altogether coincide with the view, which has by now become somewhat stereotyped, of a somewhat mechanical differentiation of growth-forms according to the local variations of an all-powerful environment. On Yonge Reef there exists, it is true, a great array of squat forms near the breakers—forms so solid that it is hard work to detach them even with a strong cold chisel; but against this we have to set the fact that in this same environment there occurs the delicate *A. delicatula*,* flourishing perfectly well; and the further fact that the heavy forms persist to leeward of the reef, though possibly in a less extreme form. Also, the reef crest, which must be considerably wave-swept at some states of the tide, bears a certain amount of actual staghorn coral, though not of the most straggling types. This account follows the traditional one only in so far as we agree that large and straggling staghorn types cannot occur in the wave zone; and conversely that low-growing forms are characteristic of this zone.

Some of the points just mentioned, together with further ones, are illustrated in Plates IX and X. In Plate IX, fig. 3, we see the extreme of reduction of the branches of a species of *Acropora* (probably *A. gemmifera*) to short cones (this photograph was taken near the outer ridge); in fig. 4 a colony of *A. gemmifera* from the leeward side of the reef, in which the branches in the centre are still very short and stumpy. In Plate III, figs. 3 and 4, and Plate X, fig. 5, are seen intermediate conditions of the same species, and in Plate IX, fig. 1, a colony of it from sheltered water at Low Isles. The type of variation which may legitimately be expected† within the limits of a single genuine species is illustrated by this series; the effect of environment is there, but is correlated only in a general way,

* Matthai identifies this species as *A. delicatula*, in which case our specimens are presumably young colonies of a species which ultimately becomes bracket-like. It is a possibility, however, that our examples are in reality adult; but only another visit to the reef could settle the point.

† I am aware that by reproducing photographs of several specimens of a single species (especially in the case of *A. gemmifera*) I am laying myself open to the criticism that, in the opinion of a given systematist, my photographs represent, not one species, but several. Such differences of opinion are inevitable in work dealing with the species in difficult genera. In these cases I have consulted the systematic literature carefully, and feel that there is good ground for my view. It may be noted in this connection that weight should be given to the experience of the field-worker who has seen the species growing in its hundreds, as well as to the opinion of the purely systematic worker. With reference to the present figures, even if they did not all represent *A. gemmifera*, *sensu stricto*, they would still illustrate "the type of variation which may legitimately be expected within the limits of a single genuine species."

and not in detail, with the form of the coral; specimens almost exactly like Plate IX, fig. 1, could be procured on the same coral head as the one shown in fig. 4, and moreover, stumpier forms are to be found in the Low Isles anchorage (one of the most sheltered parts of a sheltered reef), as is witnessed by Plate III, figs. 3 and 4. Next, in fig. 7 on Plate X we have the aforementioned *Acropora delicatula* from the outer moat. This has the wrong characteristics for a rough-water coral, measured by the Wood-Jones criteria; instead of a dense compact structure, with corallites flush with the surface, it has slender breakable branches, which have prominent lateral corallites. Again, Plate X, figs. 6 and 8, show two examples of *A. hyacinthus*, one from the most sheltered part of Low Isles, the other from the outer ridge of Yonge Reef; there is certainly a difference between them—a thickening up of the breaker-zone specimen; but the difference is by no means of the magnitude which should be expected according to the Wood-Jones view (see below). Lastly, in figs. 1 and 2 on Plate X we have an example of a fairly frequent occurrence, which is definitely against an environmental interpretation. In fig. 1 we have a fairly normal branch of *Acropora squamosa*; in fig. 2 a totally different one, which could easily be identified as belonging to a different species; yet both specimens belonged to one and the same colony. The transition from branches of one type to branches of a different build is also shown in the case of another species, in Plate IX, fig. 4. The case of figs. 1 and 2 cannot be dismissed simply as the effect of the regeneration of a new type of branch on an injured colony; it is to all appearance an example of actual variation, within the same colony, having no connection with environmental effects.

It is now possible to examine some of the conclusions of Wood-Jones more closely; and this will be done most conveniently by quoting passages from 'Coral and Atolls,' and commenting upon each in turn:

1. "From the study of the life of the colony in different surroundings, and from the repair of injury, and death, in unsuitable habitats, I think it will be seen that the number of the true species of corals is by no means so great as is at present supposed. There is no doubt that a great number of our museum-made species are mere vegetative varieties, produced in response to the demands of the environment" (p. 131).

With much of this I agree entirely.

2. "though a definite inherent growth tendency is strongly implanted in the embryo, still the demands of the environment may call forth *any type of vegetative growth*" (p. 72; italics mine).

This statement certainly needs modification. The environment cannot call forth "any type of vegetative growth"; it can merely induce certain variations, within definite limits; and although the "inherent growth tendency" is admitted in the quotation, it is in fact given comparatively little weight in the book, whereas it is in reality very important.

3. "Totally different forms are produced in totally different environments, but these forms must not be regarded as "species," for they are mere variations of vegetative growths in response to the necessities of the life-surroundings of the colony" (p. 93).

This is justified if understood in the light of the modification introduced under no. 2, but hardly, as we shall see, in the degree in which it was intended by its author.

4. "The rough-water forms of the *Madrepora* are highly characteristic, and all depend on the processes which always occur in this group when the "dominant apical zooid" is injured" (p. 88). "all these rough-water forms are in reality the result of perpetual injury" (p. 87).

There is no evidence in favour of these statements, and our work definitely points the other way. Wood-Jones has shown, it is true, that if terminal polyps are injured (and especially when the damage affects a large area of a branch), branching from lower down is stimulated; but it is not simply a repetition of such processes which produces the squat forms of rough water. A sufficient number of successive injuries to apical polyps would undoubtedly produce a curious colony, probably highly branched, and possibly with many of the branches incipient rather than properly developed; but the aspect of such a colony would not be the same as that of a normally produced stumpy colony, or if it were, the resemblance would be secondary and accidental. There appears to me to be no doubt that the ordinary squat, but often beautifully symmetrical forms of rough water are the result of the working together of two influences, (1) an inherent tendency to a certain degree of squatness, and (2) the gradual and normal growth of the colony under the action of the surf. This latter factor appears constantly to inhibit and hold in check the growth of the coral, with the result that the growth is restrained instead of exuberant, and results in compact instead of straggling forms of growth. As we have seen, however, such forms need not necessarily be of strong or massive texture, nor are massively branched forms by any means confined to rough water.

5. "it is diagnostic of a rough-water coral that its structure is compact and dense, and its corallites tend to be flush with the general surface of the growth" (p. 90).

This remark is expressed as a matter of tendency, and is therefore probably not intended to admit of no exception; but the exception provided by *Acropora delicatula* is such a striking one as to involve some modification even of a general statement. *A. delicatula* has a compact profile, certainly, and its branches are close-set, with a strong base; but its actual structure is not compact and dense, but light and breakable; and its corallites are decidedly of an angular and projecting type.

6. "In the smooth-water forms the predominant feature of the colony is the fragile nature of the growth." "Their branches are long and slender, their structure is far more porous, and their whole appearance is quite different from that of the colonies of the same species that chance to reside in wave-beaten areas" (p. 92).

These statements need modification to suit the facts that (1) solid massive forms (even of *Acropora*) are common in sheltered water (2) delicate fragile forms (though not with long branches) may occur in rough water.

7. "the actual structure of the coral depends greatly upon the presence, or absence, of sediment." "Sediment will alter the appearance of a coral more strikingly than any other influence" (p. 94).

Here, I think, as well as elsewhere in the book, Wood-Jones exaggerates the evil effects of sediment. That sediment can be, and is, harmful to a certain proportion of corals under certain circumstances I do not question. But the experiments carried out at Low Isles by Marshall and Orr (described in Vol. I, No. 5, of these reports) show clearly that many corals possess unexpectedly strong powers of ridding themselves of sediment, and that, in the ordinary circumstances of their lives, when there is usually (except in deep water) at least some water-movement to supplement the activity of their cilia, sediment cannot be considered as holding the dominant position, as a lethal factor, assigned to it by Wood-Jones. Its importance will vary with different species and with different individual colonies; but speaking generally, it cannot be included among the most important and detrimental factors to which corals are exposed, except perhaps on the mud-covered

deeper portions of the seaward slopes of certain reefs, and during the infancy of corals, when they may be less able to cope with it than later on. Further, the detailed effects on coral texture claimed by Wood-Jones as the effect of sediment are distinctly non-proven.

In connection with the *general* form of the colony, reference may be made to the historic question of the colonies with dead flattened tops which have so frequently been noticed on reefs. These are attributed by Wood-Jones largely to the action of sediment. Undoubtedly at Cocos Atoll their distribution appears to support this view. At Low Isles, on the contrary, where such colonies are also common, the great majority of them occur in shallow pools on the reef flat, and the general level of their dead tops is so nearly coincident with the level of low water (varying a little with species) that it seems self-evident that they are the result of the death of the upper surfaces of the colonies, consequent upon the projection of the latter above the surface during the period of low water. Wood-Jones maintains that exposure to sun and air does not as a rule kill corals; but this is not our experience. We saw on Yonge Reef (and this was during the cooler part of the year) many colonies which had undoubtedly been killed by exposure during a few days of low spring tides; the same thing was observed at Low Isles, after a spell of hot weather, though the numbers affected were smaller. It is possible to recognize such newly killed corals by their clean white colour; they remain in this condition for a few days only after death, and then become overgrown with algae and brown with sediment. The fact appears to be, that although many colonies do survive exposure for quite a long succession of periods of low water (extending in some cases over years) after they have begun to project above the surface, other colonies which are perhaps less hardy succumb more rapidly. That the exposure wins in the end and kills the projecting parts of all of them, in certain types of surface-pools, is demonstrated by the endless succession of flat-topped platforms in the Low Isles moats. This does not mean that flat-topped colonies are never the work of sediment; a proportion of them may be, and probably are, due to it; but many are due to other causes, among them exposure; and probably in shallow water damage due to wave-borne fragments (also postulated by Wood-Jones), resulting in colonization of the wound by algae, is of more importance than the effect of sediment itself.

8. "we cannot foretell that a young colony of *Pocillopora* will certainly be *P. brevicornis* and not *P. nobilis* for, depending on the conditions of its surroundings, it might chance to be either" (p. 103). "I do not doubt either that all the forms of *Pocillopora* which are found in the atoll are in reality one species" (p. 133).

Now many of the extracts given above appear eminently reasonable, and mostly require modification rather than refutation. But in the last two quotations we reach the root of the matter, for it is in the application of the general principle to particular cases that the author appears to me to be wide of the mark, and to reveal the degree to which he has overstressed the environmental influences. Wood-Jones interprets his results as meaning that (to take a single instance) the corals represented in his figs. 25, 26, 32 and 33 all belong to one species. I should maintain, on the contrary, that even allowing for the maximum possible variation due to environment, they differ from one another in ways which are not connected with the environment, and which indicate the presence of more than one species among them; and that the same applies in other examples.

It appears to me, in fact, that Wood-Jones's observations are of great value, but that his conclusions have been somewhat vitiated by two factors:

(1) The fact that the seaward part of the barrier at Cocos Atoll happens to possess a less varied population of coral than may occur in corresponding parts of some other reefs, such as Yonge Reef, so making Cocos Atoll an imperfect basis for generalization.

(2) A failure to discriminate between those variations which are of specific value and those which are connected with environment.

If these two conditions had been altered, there would probably have been very little to choose between our views.

The conclusion, then, of both Dr. Fraser* and myself is this : That species undoubtedly exist among corals ; that they exist in considerable number ; that the growth forms and variations of detail to be found in any one species may also be considerable, but that after sufficient experience in the field, it is possible for a worker with a trained eye to determine in a great many cases which of the variations are specific and which are not ; that of the non-specific variations some are due to environmental causes, but that the effects of environment may easily be overstressed ; and that some of the variations are due to causes as yet unknown.

This does not mean that even the most experienced worker could identify every colony met with on a reef. There would be many which would defeat him, because the limits of variation are not by any means fully known as yet. But he would be able to distinguish *Acropora squamosa*, for instance, from any other species in a high proportion of cases. We feel there is very little doubt that the corals referred to in this paper by specific names do in fact represent entities of some definite description, for which the term "species" in its ordinarily accepted sense† is the most convenient term. Even if we suppose, for the sake of argument, that under some of our specific names we have in reality grouped a number of "micro-species" ; that here and there we have referred a colony to the wrong species altogether ; or that we have used for some of our species names to which they are not entitled ; still, these errors would not affect the main issue in the least (and needless to say every effort has been made to avoid them).

In choosing the photographs reproduced in the plates belonging to this paper, one of our aims was to illustrate some of the changes in form which may take place during the life-history of a single colony. Information of this description should prove useful to anyone whose task it is to attempt the identification of corals, since one of the difficulties which besets him is that of knowing what kind of allowance to make for the age of any colony which he may be studying. A study of the plates and their descriptions will show how, even among the small selection illustrated, the branches of some of the species maintain a fairly constant appearance though the form of the colony may change ; whereas in other cases the appearance of the branches alters quite definitely with increasing age.

Lastly, there is a factor in the situation which cannot be discussed fully here, since the evidence is not yet ready for publication ; but it will be shown in later reports in this volume, by S. M. Manton and by the present author, that certain coral species arrange themselves in the manner of so many other marine organisms, according to a distinct vertical zonation, on the reef. This factor possibly introduces a still further complication

* Dr. Fraser has, of course, read the manuscript of this paper.

† I cannot use space here to describe the sense in which I am using the word "species," but have attempted to explain this in another paper (1929, p. 163).

into Wood-Jones's arguments, because unless it were appreciated during a period of work on any reef, its effects might lend apparent but ephemeral support to arguments dealing with the general effects of environment.

SUMMARY AND CONCLUSIONS.

(1) The experiments described in this report dealt with the activities of 246 corals. They were carried out at Low Isles, Queensland, between July, 1928, and June, 1929. Four different experiments concerned with growth or regeneration were undertaken.

(2) The first experiment dealt with 169 corals, which were attached to concrete blocks and planted out on the reef in pools situated within 100 yards of the habitats from which they had been collected. These corals were all kept in two fenced-in pools, one in the anchorage and the other in the Western moat, the former representing an environment very favourable for coral growth, the latter a habitat subject to greater extremes of climate and suitable for the growth of a few species only. The growth of these corals is recorded during a period somewhat exceeding six months. It was found that the branching forms (*Psammocora*, *Pocillopora*, *Acropora* and *Montipora*) added, on an average, from 33 to 95% to their original diameter during this period; the average increase for these genera being summarized in the table on p. 179. It was also found that the average increase for massive corals belonging to the Astracidae (*Favia*, *Coeloria*, *Lobophyllia*, *Symphyllia*, *Galaxea*) was much smaller than that of the branched forms (10%), but that the average for massive forms of *Porites* was greater than that for the Astraeids (17%). The various data obtained from this experiment are described on pp. 174–183.

(3) The second experiment dealt with 11 colonies only. Each of these was divided into halves; one half was kept in the moat and the other in the anchorage, both halves being attached to concrete blocks as in the first experiment. The results of this procedure are described on pp. 183–5, and it is concluded that in all probability those species which are normally inhabitants of the moat will grow well both there and in the anchorage, but that the species which normally inhabit the anchorage either will die under the more stringent conditions of the moat, will grow there less well, or will fail to attain normal size.

(4) The third experiment dealt with 30 colonies, which were marked *in situ* by a diver working below the level of low water, near the mouth of the anchorage. Details are recorded (pp. 185–8) referring to 11 of these colonies which were recovered after the experiment, and in which branches had been broken off, so that data concerning regeneration might be obtained; 144 regenerated branches were available for observation. The details of regeneration in *Acropora* are described, and it is shown that at least in the case of colonies of the irregular stagshorn type of growth, the amount of regeneration which takes place in individual healthy branches within a given period may be so different, that the new growth on one branch may be nearly ten times as great as that of another branch belonging to the same colony.

(5) In the fourth experiment (pp. 188–190) a variety of clean materials were fixed at various points on the reef, in the hope that coral planulae would settle upon them. About 40 young colonies established themselves on these materials, and 36 of these were recovered for measurement. The majority belonged to the species *Pocillopora bulbosa*, and it is shown that this species may form a flat expansion with diameters such as 11.0 ×

10.0 or 14.5×9.5 mm. in less than eleven months; and that during this time the first branch may arise on the expansion, attaining a height of 7 mm. and becoming trifid at the tip. Of the remaining colonies 7 belonged to the genus *Porites*, and the largest of these had formed expansions measuring 7.0×6.0 and 12.0×6.5 mm. in twenty-seven weeks.

(6) A number of the factors which influence the growth of corals are discussed (pp. 174-8) in connection with the results of the principal experiment. The conclusions may be summarized as follows:

(i) It has been shown clearly by Wood-Jones, Mayor and Edmondson that corals do not grow at an even rate, but by fits and starts, periods of growth alternating irregularly with periods in which there is little or no growth. The effects of this factor can be detected in the present experiments also, but it is possible nevertheless to distinguish more or less clearly between the effects of this and of other factors. This irregularity is best counteracted in experiments by continuing them for as long as possible; but the exact length of the experiment (within a few weeks) is of little significance, so long as it is not too short.

(ii) A coral may grow more actively in the anchorage (a favourable environment) than in the moat (a less favourable one); but the incidence of this factor varies very much according to species, and has apparently little effect in the case of corals whose normal habitat is the moat.

(iii) Small colonies of a species tend to grow more rapidly than larger colonies of the same species (this is confirmed by Mayor and Vaughan); but, except in the sense that when a colony has reached its maximum size it will grow no more, this rule does not apply rigidly and exceptions to it occur.

(iv) Individual variation appears to be a factor of importance. Corals belonging to the same species, and growing in the same environment for the same length of time, may grow at very different rates (irrespective of the size-factor); but the effects of individual variation and of irregularity of growth-rate are not easily disentangled.

(v) The form and internal structure of a colony should clearly affect the rate of growth, in the general sense that a branched species should grow more rapidly than a massive one, and one with light and slender branches more rapidly than one with stout, compact branches. This general tendency is confirmed by the results but has its exceptions.

(7) In the corals measured for the principal experiment, it was noticed (p. 181) that the average percentage increase in diameter for each of the principal genera was always higher in the case of the lesser of the two diameters measured than in the case of the greater. It is suggested that this may be due to a tendency on the part of the corals, when they can grow freely in all directions, to cover a more or less circular area, the coral growing more rapidly where it is narrower until this is attained. Certain data obtained from regenerating corals (p. 188) also suggest that if the symmetry of a colony is interrupted by damage (in a branching form), the branches which are regenerated, or which grow out from neighbouring branches, to fill the gap, grow rapidly until symmetry is restored.

(8) Some of the colonies of *Favia* and *Lobophyllia* used in the first experiment provided details of the asexual reproduction which had taken place in them during the experiment

(pp. 190–199). In the case of 6 colonies of *Favia*, the progress of 259 polyps was followed, and it was found that after about 8 months 158 of these had remained undivided, 77 had divided into two, 18 into three, and 6 into more than three new polyps, the total number at the end of the experiment being 394. In the case of 6 colonies of *Lobophyllia*, in which the polyps are much larger than in *Favia* and are meandrine in shape, there were 12 polyps to begin with, and these had increased to 16 at the end. The 12 original polyps had 47 mouths between them, but this number had increased to 59 after about 7 months. It is concluded that the reproduction in both genera was the result of intra-tentacular budding (at least in the majority of polyps), that no fission was involved, and that the new mouths were formed *de novo* and not split off from old ones.

(9) An account is given (pp. 201–3) of the distribution of the growth-forms of corals on one of the reefs of the Outer Barrier. It is maintained that this distribution calls for some modification in certain ideas which are prevalent concerning the relation between environment and growth-form in corals. Coupled with this is a discussion of the well-known views of Prof. F. Wood-Jones on the subject of species and forms of growth in corals; the conclusion is reached that species in the ordinarily accepted sense of the term do exist in many coral genera in considerable number, and that many of them may be fairly easily recognized in the field; and that Wood-Jones has considerably overstressed the effect of environmental conditions on the corals, although such an effect certainly exists, and is responsible for a considerable range of variation.

TABLES OF MEASUREMENTS.

EXPERIMENT I.

In the following table, under each species or variety, corals kept in the anchorage pen are listed first, those kept in the moat pen afterwards; corals of the same species, kept in the same pen, are listed in order of size, starting with the smallest, and taking the initial greater diameter as the index-figure. The numbers in column 1 of the table are numbers which were engraved on the cement blocks; therefore if a coral is numbered 62*a*, this indicates that it was attached to block 62, but that this block had more than one coral fastened to it, the colonies being distinguished as 62*a*, 62*b*, etc. In cases where no "remarks" occur in the last column, it may be assumed that the growth of the coral was normal. Percentages are expressed to the nearest whole number, except in the case of those below 1%.

EXPERIMENT II.

In this experiment a number of colonies were divided into halves. The system of reference numbers adopted for the halves was as follows: The letter A denotes a half-colony whose complementary half bears the symbol B. Thus, when a given colony was divided, one half was called A1, the other B1; in the case of a second colony, one half was A2, the other half B2; and so on. In the table, the series of measurements applying to the two halves of any one colony are included immediately following one another, so that the results for the two halves may readily be compared.

EXPERIMENT I.

A = anchorage; M = moat. Measurements in centimetres. See also note on p. 209.

Reference No.	Genus.	Species.	Place of origin.	Pen in which kept.	Period of growth.		Initial greater diameter.	Increase on greater diameter.		Initial lesser diameter.	Increase on lesser diameter.		Remarks.
					Weeks.	Days.		Actual increase.	Percentage increase.		Actual increase.	Percentage increase.	
62a	Acropora	<i>squamosa</i>	A	A	29	2	9.07	9.60	106	8.20	8.61	105	
61a		"	A	A	29	2	10.72	3.10	29	10.11	5.41	54	
40a		"	A	A	29	6	14.35	4.14	29	13.36	3.50	26	
7		"	A	A	30	1	21.13	7.37	35	16.21	6.40	39	
1		"	A	A	30	1	21.34	7.62	36	16.26	6.91	42	
57		"	A	A	29	2	24.00	8.26	34	21.46	7.24	34	
59		"	A	A	29	2	24.08	9.02	37	21.08	6.55	31	
35b		"	M	M	34	5	4.29	6.45	150	4.17	7.70	185	
64b		"	M	M	33	3	6.59	5.11	78	6.45	3.40	53	
63a		"	M	M	23	4	7.49	0.91	12	4.62	1.55	34	Died before end of experiment.
17b		"	M	M	34	6	12.22	3.53	29	8.03	1.80	22	Growth subnormal. Dead by end of experiment.
19		"	M	M	35	1	13.72	0.84	6	7.01	2.64	38	
35a		"	M	M	34	5	15.01	2.62	17	10.54	2.46	23	
62b		<i>quelchi</i>	A	A	29	2	8.08	7.19	89	7.75	6.78	87	
60a		"	A	A	26	5	10.85	6.15	57	10.13	7.90	78	
40b		"	A	A	29	6	11.20	4.88	44	9.96	3.36	34	
4		"	A	A	30	1	15.16	7.01	46	11.86	6.78	57	
56		"	A	A	29	5	16.18	6.43	40	15.19	4.47	29	
68c		<i>quelchi</i> , var. 1	M	M	33	4	4.37	2.24	51	2.61	2.01	77	Growth subnormal. Dead or nearly so by end of experiment.
63b		"	M	M	32	2	5.16	3.07	59	4.24	2.74	65	Died before end of experiment.
68a		"	M	M	22	1	5.61	2.08	37	5.16	1.37	27	Died before end of experiment.
68b		"	M	M	33	4	5.87	2.54	43	3.71	3.53	95	Died before end of experiment.
67b		"	M	M	22	1	6.20	1.40	23	5.94	0.97	16	Died before end of experiment.
64a		"	M	M	22	0	8.95	3.78	42	8.28	3.48	42	"
65a		"	M	M	33	4	9.55	4.57	48	6.07	2.79	46	"
65b		"	M	M	33	4	9.80	4.32	44	9.17	5.87	64	"
55a		<i>quelchi</i> , var. 2	M	A	28	0	8.51	2.69	32	7.85	4.51	57	"
58		"	A	A	29	5	12.37	8.10	65	11.79	8.23	70	"
38a		<i>pulchra</i>	A	A	27	6	8.99	7.44	83	8.99	9.68	108	"
37		"	A	A	29	6	15.72	11.33	72	14.61	11.81	81	"
51		"	A	A	29	5	15.98	11.40	71	14.94	10.34	69	"
3		"	A	A	30	1	28.07	3.61	13	25.88	8.58	33	"
95		<i>exilis</i>	A	A	27	6	18.10	9.09	50	16.56	9.47	57	"
5		"	A	A	30	1	23.85	8.66	36	14.55	3.33	23	"
97		<i>formosa</i>	A	A	27	6	22.02	8.46	38	18.59	8.69	47	"
43b		<i>gemmifera</i>	A	A	28	0	11.05	4.29	39	8.53	4.90	57	"
6		"	A	A	30	1	13.97	3.20	23	13.84	1.80	13	"
60b		<i>hyacinthus</i>	A	A	26	5	7.06	6.99	99	6.22	7.90	127	"
55b		Not determined	A	A	28	0	3.66	2.44	67	2.54	4.01	158	"
67a		"	M	M	22	1	5.16	1.37	27	3.58	3.12	87	Died before end of experiment.
66b		"	M	M	33	4	5.84	1.27	22	5.38	3.96	74	Died before end of experiment.
66a		"	M	M	22	1	6.38	2.21	35	3.43	1.07	31	"
63c		"	M	M	32	2	6.45	2.92	45	5.99	1.66	28	"
8		"	A	A	26	6	18.21	0.02	0.1	17.42	0.76	4	"
44		<i>ramosa</i>	A	A	29	6	15.32	6.43	42	11.73	6.15	52	"
81a		"	M	M	31	2	1.83	2.49	136	1.42	3.23	227	"

74	"	"	M	33	1	14.30	3.23	23	12.37	4.09	33	(Growth subnormal. More or less completely dead by end of experiment. Probably part was broken off.
76a	"	"	M	33	1	16.31	4.11	25	11.63	5.05	43	
71	"	"	M	33	1	19.89	9.88	50	16.36	10.41	64	
96	"	foliose form	A	26	6	19.52	3.76	19	17.02	0.28	2	
93	"	"	A	27	6	33.35	7.01	21	24.66	13.34	54	Somewhat broken, but a very healthy colony.
78b	"	"	M	21	4	19.05	0.64	3	15.32	1.37	9	Growth subnormal. Colony unhealthy; died before end of experiment.
9a	<i>Porites</i>	Massive; not determined	M	32	3	7.14	0.56	8	6.36	0.43	7	
20	"	Ditto	M	35	1	8.26	1.83	22	8.10	1.91	24	
48a	"	"	M	33	0	8.69	0.71	8	7.77	0.43	6	
26	"	"	M	35	1	9.55	2.46	26	9.25	3.43	37	
21b	"	"	M	35	1	13.41	1.98	15	8.59	1.63	19	
2b	<i>Pocillopora</i>	<i>bulbosa</i>	M	31	1	6.90	3.38	49	5.51	3.58	65	
27b	"	"	M	35	0	7.49	4.65	62	7.01	5.64	80	
17a	"	"	M	34	6	8.08	4.88	60	6.91	5.45	79	
81d	"	"	M	31	2	10.59	4.45	42	9.78	3.20	33	
27a	"	"	M	35	0	10.90	3.28	30	8.86	4.14	47	
32	"	"	M	35	0	11.02	5.31	48	10.31	5.59	54	
14	"	"	M	34	6	11.18	4.04	36	10.19	5.00	49	
28	"	"	M	35	0	13.69	4.04	30	13.39	4.62	35	
96	"	"	M	32	3	14.22	4.75	33	8.59	3.86	45	
34	"	"	M	34	6	15.54	4.42	28	9.73	6.86	71	
13	"	"	M	34	5	17.25	2.39	14	12.24	5.00	41	
25	"	"	M	34	5	19.66	4.29	22	17.91	5.18	29	
31	"	"	M	35	0	21.59	5.08	24	19.61	3.96	20	
30	"	"	M	34	6	27.33	3.66	13	22.66	No second measurement		A good deal was broken off during the experiment.
94	<i>Seriatopora</i>	<i>hystrix</i>	A	26	5	31.45	5.84	19	24.61	7.14	29	
81b	<i>Favia</i>	<i>doreyensis</i>	M	31	2	6.86	0.76	11	6.07	1.35	22	
48b	"	"	M	33	0	9.27	0.83	9	7.82	0.89	11	
80a	"	"	M	31	2	12.29	0.57	5	11.76	1.07	9	
70	"	"	M	33	1	16.08	1.22	8	14.73	1.19	8	
77b	"	<i>fuscus?</i>	M	33	0	5.26	0.23	4	3.36	0.66	20	
81c	"	<i>fuscus</i>	M	31	2	7.57	0.30	4	7.06	0.48	7	
2a	"	"	M	31	1	9.65	1.07	11	5.59	0.89	16	
29	"	<i>halicora</i>	M	35	0	11.90	0.89	7	11.0	0.80	7	
36b	"	<i>pectinata</i>	M	34	5	5.08	0.74	15	5.16	0.41	8	
24a	<i>Favia (Goniastrea)</i>	Species 1	M	35	0	7.54	0.97	13	6.50	0.81	12	
18	"	"	M	35	1	10.82	0.94	9	10.18	0.92	9	
22b	"	"	M	32	3	13.26	1.45	11	12.47	0.51	4	
10	"	"	M	34	5	13.84	0.46	3	13.72	0.86	6	
92a	<i>Favia</i>	Not determined	A	26	5	2.69	0.38	14	2.11	0.33	16	
69a	<i>Coeloria</i>	<i>daedalea</i>	M	31	2	6.53	1.24	19	5.99	0.58	10	
12	"	"	M	34	5	13.34	1.19	9	13.34	1.19	9	
69b	"	"	M	31	2	10.31	0.66	6	7.77	0.25	3	
83	<i>Galaxea</i>	<i>musicalis</i>	M	31	2	12.85	0.74	6	6.91	1.07	15	
79	"	"	M	33	0	17.64	1.98	11	13.82	1.37	10	A patch of polyps died, but this had little effect on growth of whole. Small groups of polyps died, but general growth was not affected.
92d	<i>Lobophyllia</i>	<i>corymbosa</i>	A	26	5	5.97	1.17	20	2.24	0.46	21	
50	"	"	A	28	0	18.85	0.79	4	16.31	0.86	5	
49	"	"	A	29	5	19.38	0.84	4	17.88	0.23	1	
55c	"	Species 1	A	28	0	6.07	0.15	2	5.94	0.15	3	

EXPERIMENT I—continued.

A = anchorage; M = moat. Measurements in centimetres. See also note on p. 209.

Reference No.	Genus.	Species.	Place of origin.	Pen in which kept.	Period of growth.		Initial greater diameter.	Increase on greater diameter.		Initial lesser diameter.	Increase on lesser diameter.		Remarks.
					Weeks.	Days.		Actual increase.	Percentage increase.		Actual increase.	Percentage increase.	
54b	<i>Lobophyllia</i>	Species 2	A	A	29	5	7.37	0.79	11	6.86	0.99	14	Part of this specimen died. Nos. 85 and 86 were halves of a single large colony.
85	"	"	M	M	32	5	21.59	0.79	4	21.16	No second measurement	6	
86	"	"	M	M	32	5	21.89	0.25	1	12.24	0.76	6	
45b	"	Species 3	A	A	29	1	7.06	0.25	4	6.68	0.38	6	Not a very healthy specimen.
45a	"	Species 4	A	A	29	1	10.29	0.05	0.5	4.57	0.46	10	
46	"	"	A	A	27	6	10.85	0	0	4.70	0.08	2	
92c	"	Not determined	Batt Reef	A	26	5	4.98	1.02	20	4.60	1.04	23	Died before end of experiment. Died before end of experiment. " " " Unhealthy at first, but recovered fully later. Unhealthy at first; flourished very well later.
53a	"	"	A	A	29	5	5.54	0.97	18	5.08	0.79	16	
53b	"	"	A	A	29	5	5.87	0.89	15	4.09	0.56	14	
92b	<i>Symphylia</i>	" recta	M	A	26	5	3.40	0.64	19	3.02	0.89	29	
36a	"	"	M	M	34	5	5.49	0.61	11	4.95	0.86	17	
77a	"	"	M	M	33	0	9.22	0.86	9	8.64	0.86	10	
91	"	"	M	M	32	5	11.66	0.15	1	10.46	0.18	2	
88	"	"	M	M	32	5	16.02	0.56	3	15.39	0.76	5	
11	"	"	M	M	32	3	20.73	1.07	5	17.75	0.76	4	
16b	<i>Fungia</i>	fungites	M	M	23	4	6.55	0.66	10	5.64	0.74	13	
15a	"	"	M	M	35	1	7.75	0.86	11	6.63	0.69	10	Unhealthy at first, but recovered fully later. Unhealthy at first; flourished very well later.
15b	"	"	M	M	23	5	8.08	0.28	3	7.87	0.02	0.3	
84b	"	"	M	M	19	6	9.78	0.41	4	9.73	0.28	3	
16a	"	"	M	M	35	0	11.07	0.38	3	10.86	0	0	
47a	"	fungites, var. I	M	M	26	5	12.07	0.02	0.2	10.49	0.23	2	
98	"	actiniiformis var. crassitentaculata irregularis	A	A	27	6	17.55	0.08	0.4	18.47	0	0	
47b	<i>Döderleinia</i>	"	A	A	26	5	11.40	0.30	3	9.42	0.61	6	
52	"	"	A	A	28	0	34.34	0.66	2	24.41	0.71	3	
100	<i>Herpetolitha</i>	Species 1	A	A	26	5	26.11	0.58	2	11.84	0	0	
33b	<i>Psanimocora</i>	gonagra	M	M	35	0	5.84	3.30	57	5.56	2.71	49	
89c	"	"	M	M	32	5	7.19	2.57	36	5.41	2.84	52	Nos. 73 and 82 were portions of a single large colony.
89b	"	"	M	M	32	5	7.44	3.15	42	7.32	2.90	40	
33a	"	"	M	M	35	0	7.80	2.64	34	6.02	2.90	48	
75b	"	"	M	M	31	2	8.41	2.87	34	7.62	2.69	35	
84a	"	"	M	M	31	2	11.68	2.77	24	9.73	3.81	39	
75a	"	"	M	M	31	2	13.69	2.95	22	10.82	2.69	25	
90	"	"	M	M	32	5	17.22	3.10	18	15.19	2.77	18	
89a	"	"	M	M	32	5	17.68	2.69	15	15.75	2.13	14	
73	<i>Pavona</i>	cactus	M	M	33	1	15.24	3.81	25	14.68	2.16	15	
82	"	"	M	M	32	5	22.28	2.46	11	18.59	2.34	13	
24b	<i>Lobophyllum</i>	near crebriplicatum	M	M	35	0	12.09	7.67	63	9.12	6.58	72	Probably died soon after beginning of experiment.
43a	"	Species 1	A	A	28	0	7.82	1.55	20	7.82	1.96	26	
61b	<i>Sinularia</i>	"	A	A	29	2	5.66	3.20	57	5.21	2.24	43	
99	<i>Helopora</i>	coerulea	A	A	26	6	28.83	0.82	3	26.57	0.91	3	

EXPERIMENT II.

A = anchorage; M = moat. Measurements in centimetres. See also note on p. 209.

Reference No.	Genus.	Species.	Place of origin.	Pen in which kept.	Period of growth.		Initial greater diameter.	Increase on greater diameter.		Initial lesser diameter.	Increase on lesser diameter.		Remarks.
					Weeks.	Days.		Actual increase.	Percentage increase.		Actual increase.	Percentage increase.	
A2	<i>Acropora</i>	<i>squamosa</i>	M	A	27	0	7.19	3.68	51	6.86	5.18	76	Growth probably subnormal.
B2	"	"	M	M	31	3	7.29	1.37	19	6.83	1.50	22	
A1	"	<i>quedchi</i> , var. 1	M	A	27	0	4.90	1.73	35	4.04	2.18	54	
B1	"	"	M	M									Made no progress.
A10	"	<i>exilis</i>	A	A	26	5	15.39	6.15	40	13.00	6.10	47	
B10	"	"	A	M									Died a few days after transplantation.
A9	"	<i>formosa</i>	A	A	26	5	14.68	10.52	72	14.30	10.39	73	
B9	"	"	A	M	Was dead all but one twig 10 weeks after beginning of experiment; part of this twig survived a few weeks longer but ultimately died also.								Much broken; smaller at end of experiment than at beginning.
A8	"	<i>hebes</i>	M	A									
B8	"	"	M	M	31	3	14.17	8.42	59	16.33	7.42	45	Died slowly. Discarded 20 weeks after beginning of experiment.
A3	"	"	M	A	27	0	12.75	5.16	40	11.35	5.76	51	
B3	"	"	M	M									Died a few days after transplantation.
A7	"	Species 1	M	A	27	1	10.62	4.39	41	8.74	7.09	81	
B7	"	"	M	M	31	3	9.98	5.26	53	5.11	1.09	21	Died slowly. Discarded 20 weeks after beginning of experiment.
A5	<i>Montipora</i>	<i>ramosa</i>	M	M	31	1	13.06	3.28	25	9.02	1.70	19	
B5	"	"	M	A	27	1	12.98	7.98	61	9.56	6.35	66	Died a few days after transplantation.
A11	"	foliose form	A	M									
B11	"	"	A	A	26	5	23.22	4.67	20	20.68	5.77	28	Died a few days after transplantation.
A4	<i>Pocillopora</i>	<i>bulbosa</i>	M	M	31	1	7.90	0.99	13	3.91	3.15	81	
B4	"	"	M	A	27	1	7.58	3.05	40	6.63	2.51	38	Died a few days after transplantation.
A6	"	"	M	M	31	1	15.29	3.45	23	14.40	3.84	27	
B6	"	"	M	A	27	1	12.45	4.06	33	11.99	4.14	35	

EXPERIMENT III.

In this experiment branches were broken from a number of colonies, which were marked in the manner described on p. 173. The colonies were left growing *in situ*, the work being carried out by a diver. All the colonies were situated near the mouth of the anchorage.

Reference No.	Genus.	Species.	Period of experiment.		Method of marking.	Number of regenerating branches which had subdivided.	Lengths of regenerated portions of individual branches in millimetres. Measured from the point of fracture to the tip of the new branch. Where two or more branches were the same length, the number of these is given in brackets after the length concerned.
			Weeks.	Days.			
1	<i>Acropora</i>	<i>formosa</i>	14	0	Branches marked separately	3	3.0, 3.25, 6.0, 6.5, 7.75, 8.0 (2), 8.75, 9.5, 10.0, 10.5, 14.25, 14.5 (2), 18.5, 19.5, 21.5 (2), 23.75.
2	"	"	7	1	Ditto	0	1.5, 2.0, 3.5 (3), 5.5.
3	"	"	15	3	"	0	<1.0 (2), 1.25, 3.0, 5.0, 8.0, 8.5.
4	"	<i>gemmifera</i>	15	2	Group of branches marked	0	6.0, 6.5, 7.5 (2), 8.25, 8.75, 9.5, 10.0, 11.0, 12.0 (2). The new branches had not in the main attained the same level as the old ones. Only a proportion of the new ones could be measured, since in the rest the point of breakage could not be identified.
5	"	"	13	5	Ditto	0	3.5, 6.0, 6.5, 7.0, 7.25 (2), 7.5 (3), 7.75, 8.0, 8.25, 8.5, 9.25 (3). The new branches had not in the main attained the same level as the old ones. Most of the new branches were measurable, since the breakage point was easily identified.
6	"	<i>quelchi</i>	15	2	"	0	2.0, 4.5, 4.75, 6.75, 9.0, 10.5, 11.0, 11.5, 12.75. The same remark applies as in No. 4.
7	"	"	13	5	Branches marked separately	0	<1.0 (2), 2.5, 2.75, 3.5, 4.0, 4.25, 4.5 (3), 5.25, 5.5, 6.5, 7.0 (2), 9.25.
8	"	<i>polymorpha</i>	13	5	Ditto	6	14.25, 15.0, 17.25, 21.25, 22.75, 25.5.
9	"	"	25	3	"	2	4.0, 6.0, 9.0, 11.0, 12.0, 17.0, 17.25, 19.25, 21.0, 29.0, 33.5, 35.0, 38.75.
10	"	Species 2	13	5	"	1	5.0, 5.5, 6.0, 6.5, 7.5 (2), 8.0, 8.5 (2), 8.75, 9.0 (3), 9.5, 10.0, 10.25, 10.5 (3), 11.75, 13.5, 13.75.
11	"	" 3	13	5	"	0	<1.0 (9), 1.5, 2.0 (3), 2.75, 3.5, 5.0, 6.0, 7.5.

EXPERIMENT IV.

In this experiment coral planulae were allowed to settle upon clean materials which had been planted out on the reef. The dimensions of colonies which developed from such planulae are recorded, and measurements of certain other organisms which also settled on the materials provided are added. Most of the colonies were still in the form of flattened expansions, in which case two diameters are given, taken more or less at right angles to one another. In other cases a vertical branch had arisen; for these the height of the branch is also recorded.

EXPERIMENT IV.

See note on p. 214.

Reference No.	Name of organism.	Locality in which the larvae settled.	Period of experiment.		Diameters in millimetres.	Height of branch, when present, in millimetres.	Reference No.	Name of organism.	Locality in which the larvae settled.	Period of experiment.		Diameters in millimetres.	Height of branch, when present, in millimetres.
			Weeks.	Days.						Weeks.	Days.		
1	<i>Pocillopora bulbosa</i>	Madrepore moat	42	5	1.3	1.1	34	<i>Cyphastrea</i> sp.	Porites pond	42	5	7.4	6.5
2	"	"	42	5	2.8	2.5	35	Undetermined coral	Western moat	43	0	4.7	4.4
3	"	"	42	5	3.3	3.2	36	Ditto	Porites pond	42	5	4.0	3.3
4	"	"	42	5	3.7	2.9	37	<i>Anomia ? cytaeum</i>	Madrepore moat	14	0	10.0	8.2
5	"	"	42	5	4.5	3.0	38	"	"	14	0	17.0	15.3
6	"	"	42	5	4.5	3.5	39	<i>Pinctada panasesae</i>	Porites pond	42	5	9.8	7.8
7	"	"	42	5	5.5	5.0	40	"	Anchorage	36	2	14.9	14.8
8	"	"	42	5	5.5	5.0	41	"	"	43	0	17.9	13.4
9	"	"	42	5	6.5	5.0	42	<i>Spondylus hystrix</i>	Porites pond	42	5	11.0	9.2
10	"	"	42	5	7.0	5.5	43	"	"	42	5	12.5	11.4
11	"	"	42	5	7.5	5.5	44	"	"	42	5	13.5	11.3
12	"	"	42	5	8.0	7.5	45	"	Anchorage	43	0	17.0	16.9
13	"	"	42	5	8.5	6.9	46	<i>Spondylus ? hystrix</i>	"	43	0	12.7	11.8
14	"	"	42	5	9.0	6.5	47	<i>Ostrea cerata</i>	Porites pond	42	5	25.4	24.8
15	"	"	42	5	9.0	8.0	48	"	"	42	5	25.8	18.5
16	"	"	42	5	11.0	10.0	49	<i>Barbatia decussata</i>	"	42	5	9.4	5.1
17	"	Western moat	43	3	1.7	1.6	50	<i>Vermetes</i> sp.	"	42	5	10.0	
18	"	"	43	0	2.6	2.3	51	"	"	42	5	12.8	
19	"	"	43	0	3.5	3.4	52	"	Anchorage	43	0	11.9	
20	"	"	43	0	7.5	6.0	53	Polychaet tube	"	36	2	51.15 (length)	
21	"	Porites pond	42	5	2.7	2.6	54	"	"	36	2	134.2	
22	"	"	42	5	4.5	4.0	55	Sponge	"	36	2	62.5	13.0
23	"	"	42	5	5.7	4.9	56	<i>Gellius fibulatus</i>	Western moat	16	2	Length of individual branches	
24	"	"	42	5	10.4	7.7						65.0 (3), 75.0	
25	"	"	42	5	14.5	9.5						80.0, 95.0,	
26	"	Mouth of anchorage	12	3	1.8	1.7						100.0, 105.0	
27	<i>Porites</i> sp.	Western moat	27	1	7.0	6.0						12.0 wide;	
28	"	"	27	1	12.0	6.5						21.0 high	
29	"	"	42	5	3.6	3.1	57	<i>Retepora graeffei</i>	Anchorage	43	0	19.2 wide;	
30	"	Porites pond	42	5	3.6	3.1	58	"	"	43	0	13.0 high	
31	"	"	42	5	3.7	3.6							
32	"	"	42	5	5.4	3.9							
33	"	"	42	5	6.6	5.9							

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SYSTEMATIC INDEX

	PAGE		PAGE
Acropora	173, 179, 182, 189, 200, 207	Herpetolitha	181-2, 212
„ decipiens	201	Hormothamnium solutum	173
„ delicatula	201-4		
„ exilis	180, 183, 210, 213	Lobophyllia	179, 181-2, 194-9, 207-9
„ formosa 180, 183, 185, 188, 210, 213-14		„ corymbosa	211
„ gemmifera 180, 187, 188, 201-2, 210, 214		„ undetermined species	211-12
„ hebes	184, 201, 213	Lobophytum crebriplicatum	212
„ hyacinthus	180, 203, 210	„ undetermined species	212
„ palifera	180	Lyngbya majuscula	173
„ polymorpha	186-8, 214		
„ pulchra	180, 202, 210	Madrepora 203 ; see also Acropora.	
„ quelchi 177, 180, 184, 188, 210, 213-14		Microphytic algae	189
„ squamosa . 175, 180, 184, 187, 201, 203,	206, 210, 213	Montipora	207
„ undetermined species . . 175, 184, 210,	213-14	„ foliose species	180, 183, 211, 213
		„ ramosa	178-80, 182-3, 210-11, 213
Actinians	191	Ostrea cerata	215
Alcyonaria	181	Oysters	190, 215
Anomia cytaeum	215		
Astraeidae	181, 207	Padina	189
		Pavona cactus	181, 212
Barbatia decussata	215	Pinctada panasesae	215
		Pocillopora	179, 182, 187, 190
Coeloria	181-2, 207	„ brevicornis	205
„ daedalea	179, 211	„ bulbosa	176-7, 183, 188-9, 207, 211, 213, 215
Corynactis	191	„ nobilis	205
Cyanophyceae	173	Polychaet tubes	215
Cyphastrea	189, 215	Porites	177, 179, 182, 189, 190, 207-8, 211, 215
		Psammocora	179, 181, 182, 207
Döderleinia	181	„ gonagra	212
„ irregularis	212		
		Retepora graeffei	189, 215
Favia	179, 181-2, 191-5, 207-9		
„ doreyensis	194, 211	Seriatopora	180
„ favus	194, 211	„ hystrix	211
„ halicora	211	Sinularia	212
„ pectinata	211	Spondylus hystrix	215
„ undetermined species	194, 211	Sponge	215
Fungia actiniformis	181, 212	Symphyllia	179, 181, 182, 207
„ fungites	181, 212	„ recta	212
Galaxea	207	Turbinaria	210
„ musicalis	181, 211		
Gellius fibulatus	190, 215	Undetermined coral	189, 215
Goniastrea pectinata	211		
„ undetermined species	211	Vermetidae	190
		Vermetus	215
Heliopora coerulea	181, 212		

DESCRIPTION OF PLATE I.

(In this plate, and also in Plates II to VII, the scale is indicated wherever possible by rows of black and white squares, which represent square centimetres, and which were photographed at the same time as the corals; these squares are approximate, and do not represent the scale from which the actual measurements were made. Except in Plate VII, fig. 5, the row of squares is placed in all cases *between* the two photographs which represent the same coral at the beginning and end of the experiment; as a guide to the eye. In all cases where two photographs of the same coral are given, from the same point of view, they are to the same scale.)

GROWTH IN COLONIES OF ACROPORA IN THE HABITATS IN WHICH THEY WERE FOUND.

FIGS. 1 and 2.—*Acropora pulchra*. Experiment I, no. 37. Collected and planted out in the anchorage. This specimen showed an increase of 72% and 81% on its greater and lesser diameters respectively, during a period of 29 weeks and 6 days. The remarkable increase in the *area* covered by the coral, within the 7½ months, is obvious from the photographs. The growth-form has not changed markedly.

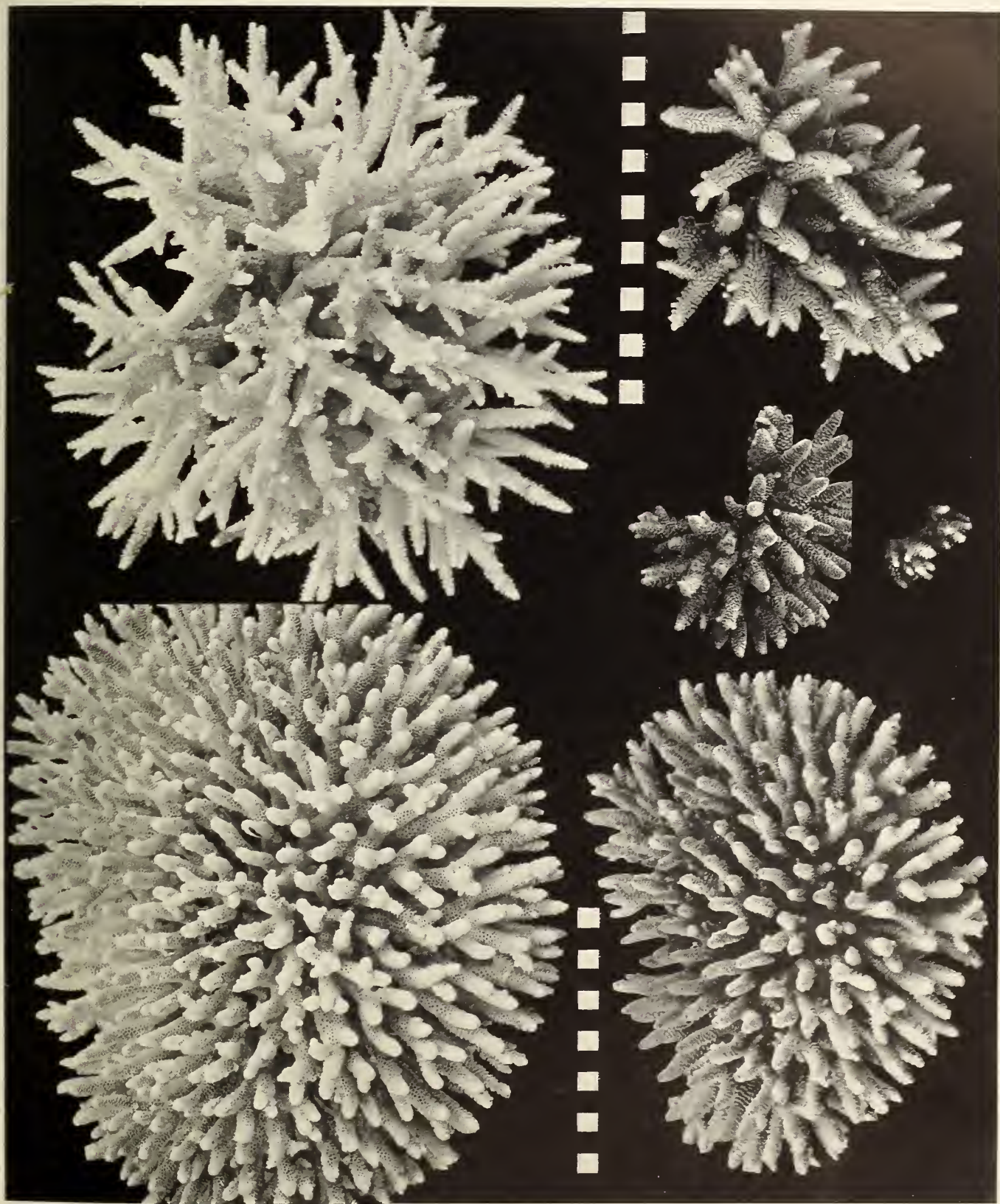
FIGS. 3-6.—*Acropora squamosa*. Figs. 3 and 4, Experiment I, no. 35*b*, collected and planted out in the moat. Figs. 5 and 6, Experiment I, no. 57, collected and planted out in the anchorage. In figs. 3 and 4 an enormous relative increase in a very young colony is illustrated (150% and 185% on the greater and lesser diameters respectively); in figs. 5 and 6 the colony was much larger at the beginning of the experiment; the increase in size is still considerable (34% on each of the two diameters), but not as great as in the case of the small colony. The period of experiment for the small colony was 34 weeks and 5 days, for the larger one 29 weeks and 2 days. The scale of the small colony is not given on the plate; its initial greater diameter was 4.29 cm. A further example of growth in this species is given in Plate II, figs. 1 and 2.

GREAT BARRIER REEF EXPEDITION 1928-29.

Brit. Mus. (Nat. Hist.).

REPORTS, VOL. III, No. 7.

PLATE I.



Photographs by T. A. Stephenson.

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DESCRIPTION OF PLATE II.

GROWTH IN COLONIES OF ACROPORA IN THE HABITATS IN WHICH THEY WERE FOUND.

FIGS. 1 and 2.—*Acropora squamosa*. Experiment I, no. 62a. Collected and planted out in the anchorage.

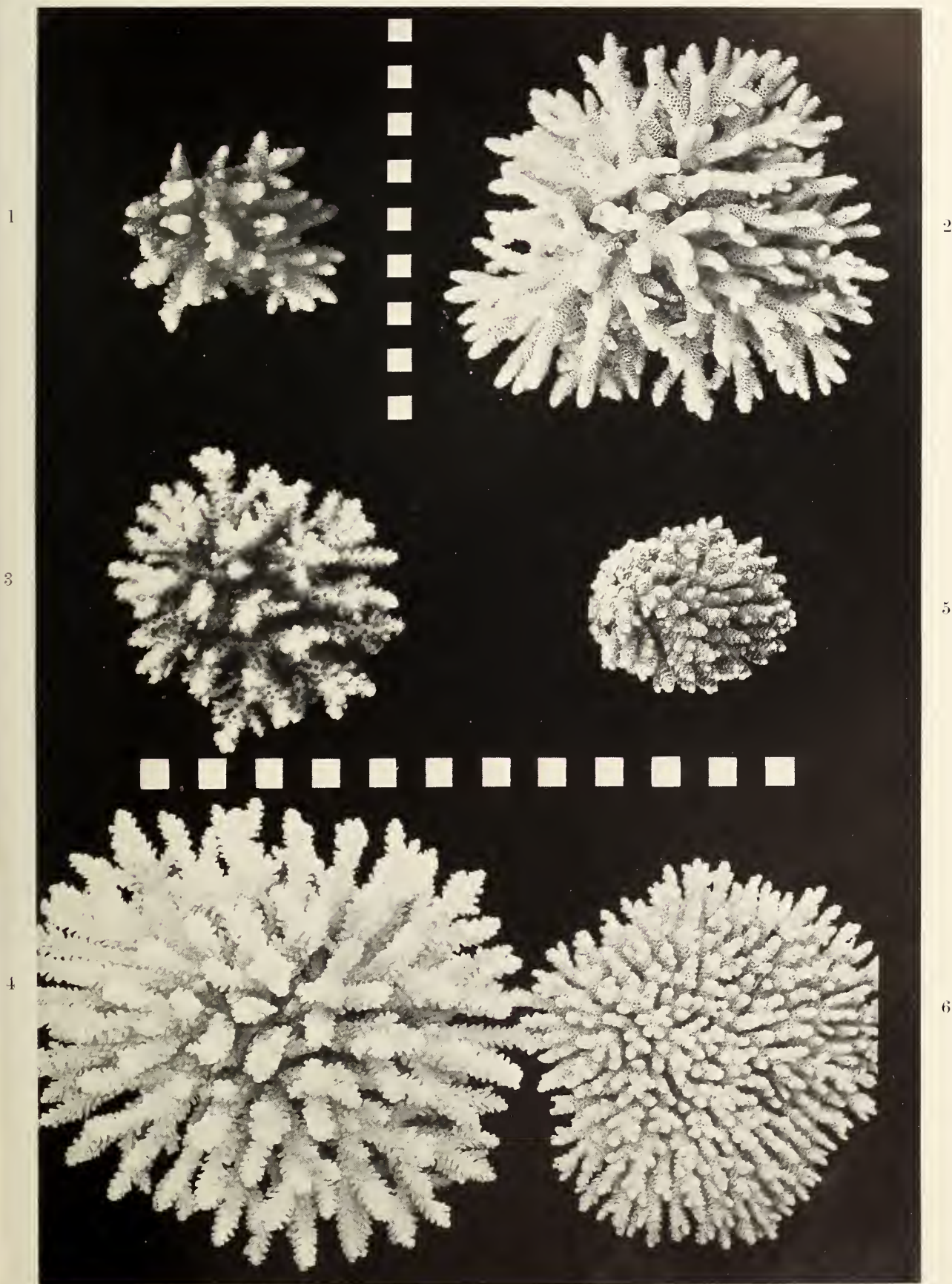
This specimen was intermediate in size between the two colonies of the same species illustrated in Plate I; and its growth was of intermediate amount (106% and 105% on the two diameters in 29 weeks and 2 days). The several photographs of this species illustrate the change from a somewhat irregular shape in the young colony, to the adult condition in which the colony forms a cyathiform or bracket-like expansion, flat on the top and with a stout stem below; but the appearance of the individual branches changes very little after the colony has attained a diameter of a few centimetres, making the species as a rule readily recognizable.

FIGS. 3 and 4.—*Acropora quelchi*. Experiment I, no. 60a. Collected and planted out in the anchorage.

Another species with branches of medium thickness in which growth is rapid. In this case the increase was 57% and 78% on the greater and lesser diameters respectively, in a period of 26 weeks and 5 days.

FIGS. 5 and 6.—*Acropora hyacinthus*. Experiment I, no. 60b. Collected and planted out in the anchorage.

This is one of the most delicately branched species of *Acropora* found at Low Isles, but is the one which grows to the largest size, frequently forming shelf-like brackets which project from the sides of rocky masses and are 6 or 8 ft. in diameter. The young colony forms a rounded bush (fig. 5); when older, if able to extend freely in all directions, it forms a vase-like structure (it has attained this stage in fig. 6, a side view of which is shown in Plate X, fig. 6); the growth subsequently tends to become less symmetrical, and the adult frequently forms a shelf attached at one side only. The increase of size in this specimen was 99% and 127% on the greater and lesser diameters in 26 weeks and 5 days.



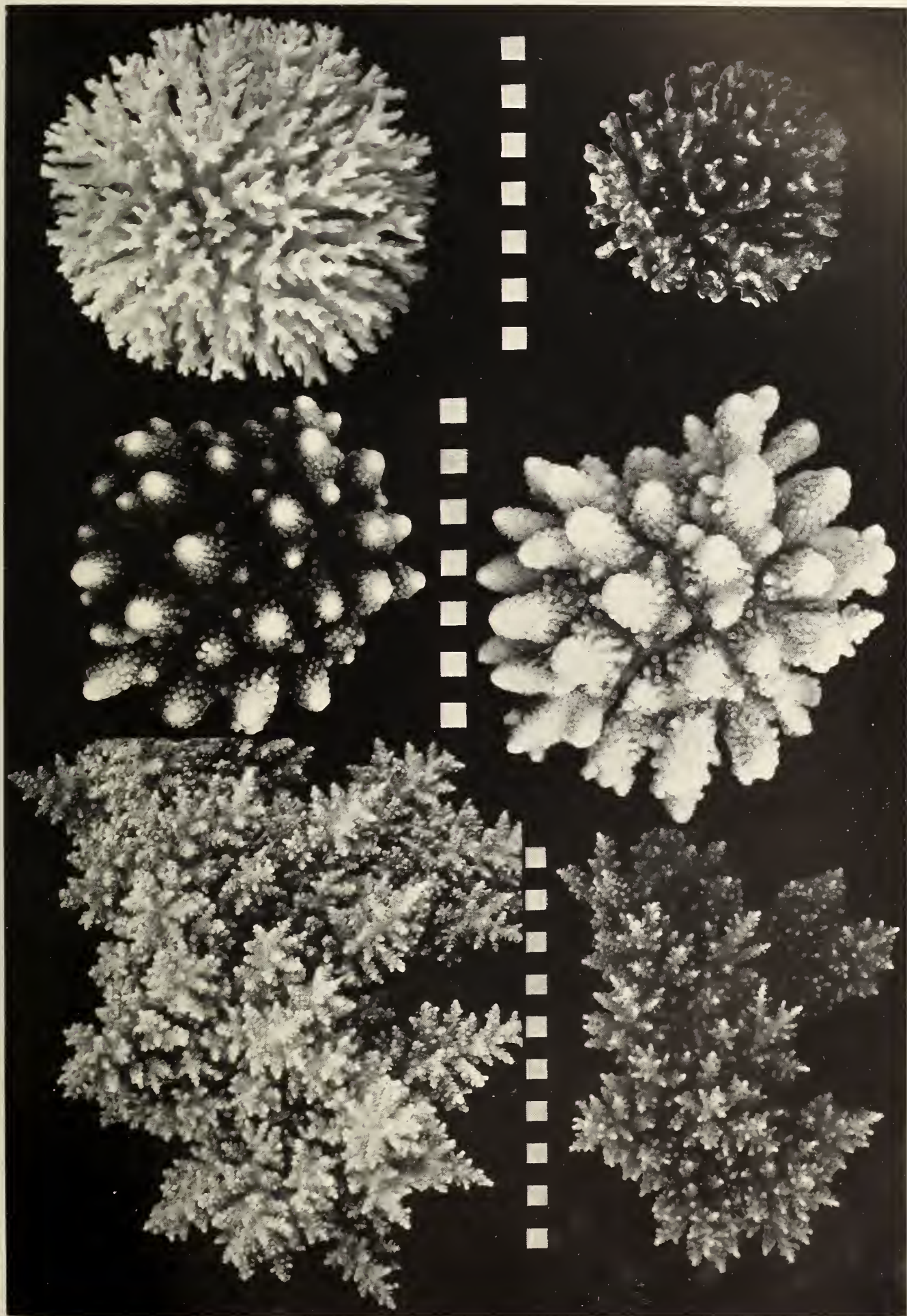
DESCRIPTION OF PLATE III.

GROWTH IN COLONIES OF ACROPORA AND POCILLOPORA IN THE HABITATS IN WHICH THEY WERE FOUND.

FIGS. 1 and 2.—*Pocillopora bulbosa*. Experiment I, no. 32. Collected and planted out in the moat. Increase 48% and 54% on the two diameters, in 35 weeks. The figures illustrate the amount of growth in a common moat-living species accustomed to high temperatures during the period of low water in the summer. The coral has maintained a similar aspect throughout the period of the experiment, which is in contrast to the change which has taken place in specimens of another common moat species in the same pool (Plate V, figs. 6 and 7).

FIGS. 3 and 4.—*Acropora gemmifera*. Experiment I, no. 6. Collected and planted out in the anchorage. Here the growth is considerably less than in the other species of *Acropora* illustrated, on account of the massive nature of the branches. The increase was 23% and 13% on the two diameters, in 30 weeks 1 day.

FIGS. 5 and 6.—*Acropora exilis*. Experiment I, no. 95. Collected and planted out in the anchorage. This species illustrates the extreme reached by the genus, at Low Isles, in the direction of a high degree of subdivision of delicate branches; and this form of growth is associated with fairly rapid increase in size (50% and 57% increase on two diameters, in 27 weeks 6 days).



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DESCRIPTION OF PLATE IV.

GROWTH IN FOLIOSE SPECIES OF MONTIPORA IN THE HABITATS IN WHICH THEY WERE FOUND.

FIGS. 1 and 2.—A foliose species of *Montipora*. Experiment II, no. B 11. Collected and planted out in the anchorage. The growth has been considerable (20% and 28% increase on two diameters in 26 weeks 5 days), and the complexity of the folding has increased as growth proceeded.

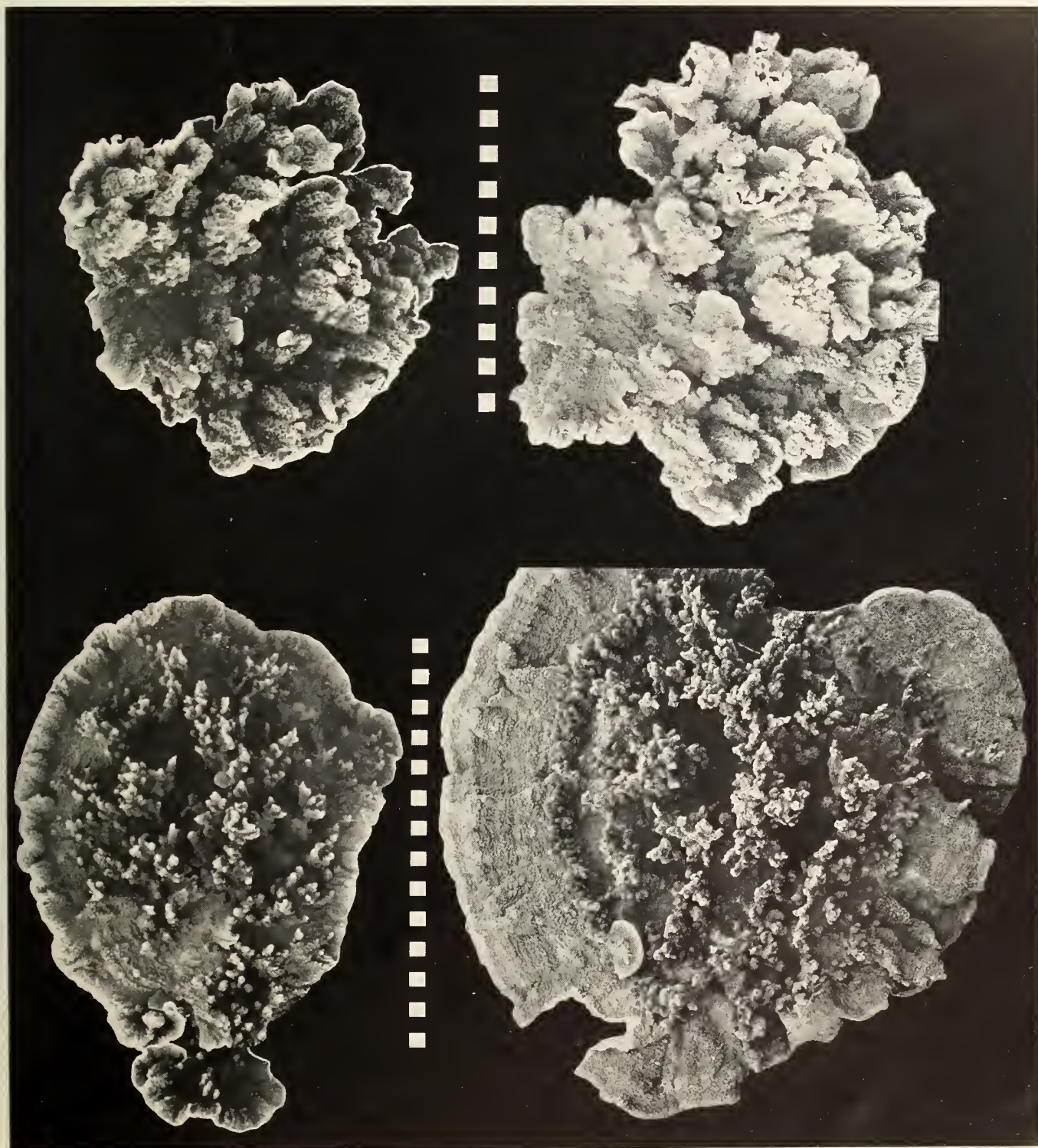
FIGS. 3 and 4.—A species of *Montipora* with upright branches in the centre and a foliose margin. Experiment I, no. 93. Collected and planted out in the anchorage. The marginal shelf has increased very much in width during the experiment; the branches have also grown upwards considerably, but foreshortening has masked this in the photograph. The increase in diameter was 21% and 54% on the greater and lesser diameters respectively, in 27 weeks 6 days.

GREAT BARRIER REEF EXPEDITION 1928-29.

Brit. Mus. (Nat. Hist.).

REPORTS, VOL. III, No. 7.

PLATE IV.



Photographs by T. A. Stephenson.

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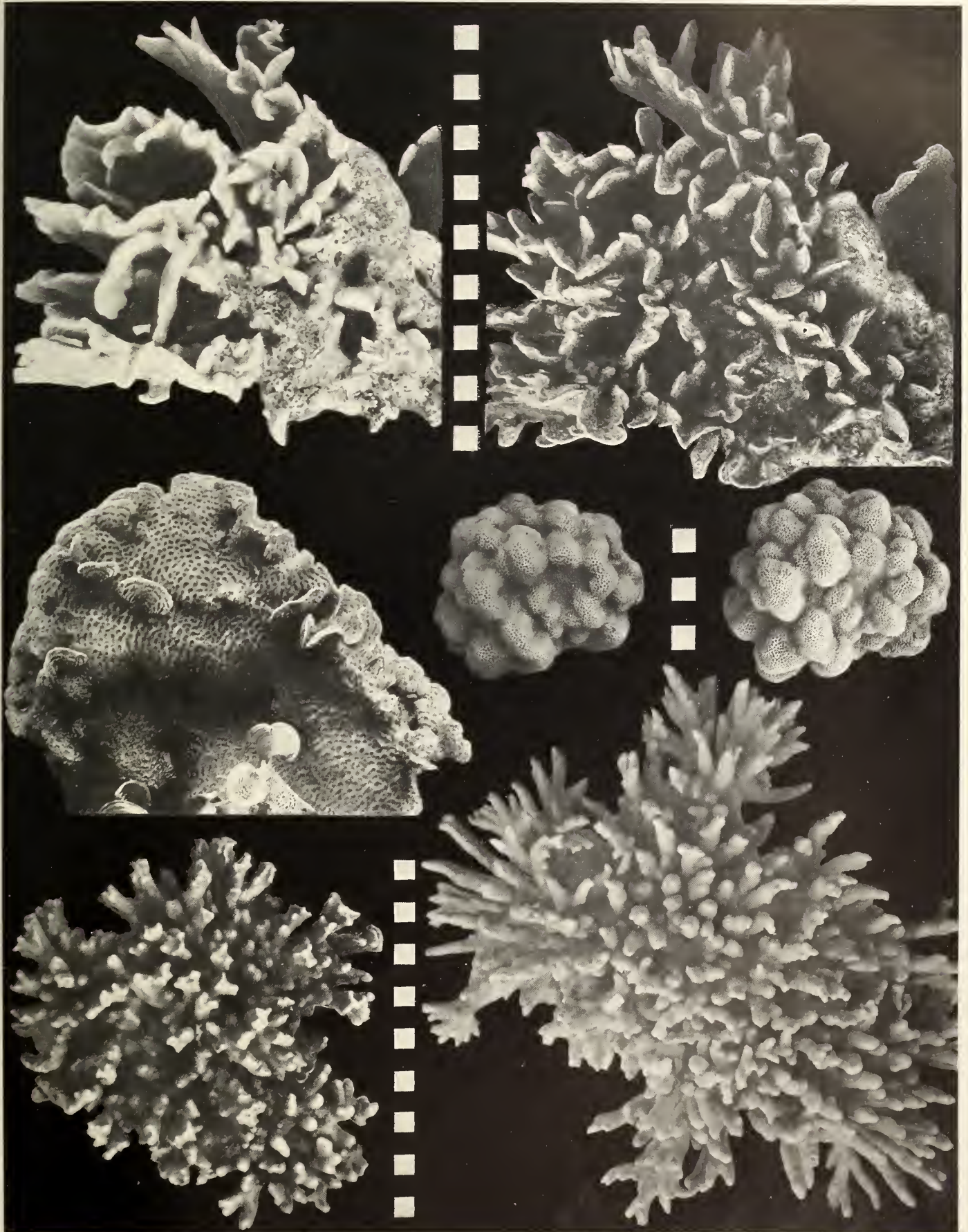
DESCRIPTION OF PLATE V.

GROWTH IN COLONIES OF PAVONA, PORITES AND BRANCHED MONTIPORA IN THE HABITATS IN WHICH THEY WERE FOUND.

FIGS. 1-3.—*Pavona cactus*. Experiment I, no. 73. Collected and planted out in the moat. This species is made up of somewhat massive vertical plates (one of which is illustrated in side view in fig. 3) with foliose margins. The specimen illustrated was part of a large colony which had shared in the formation of a platform in the western moat, part of the top of which had been killed after reaching low-water level. During the experimental period the coral not only increased in diameter (25% and 15% on two diameters in 33 weeks 1 day), but also increased the growth of small secondary plates on its upper surface (in figs. 1 and 2 it is viewed from above).

FIGS. 4 and 5.—A massive species of *Porites*. Experiment I, no. 48a. Collected and planted out in the moat. The amount of growth in this coral (an increase of 8% and 6% on two diameters in 33 weeks), is naturally much less than the amounts illustrated in Plates I-IV, because of the massive form of the coral; but is rather low compared with the increase achieved by certain other colonies of *Porites* used in the experiment.

FIGS. 6 and 7.—*Montipora ramosa*. Experiment I, no. 71. Collected and planted out in the moat. This species is one of the most characteristic of the inhabitants of the moats. Not only does it grow rapidly (the case illustrated showing an increase of 50% and 64% on two diameters in 33 weeks 1 day), but it changes markedly in aspect as it does so. From figs. 6 and 7 it can be seen that the appearance of the branches at the end of the experiment is very different from their appearance at the beginning; and from fig. 7 that the central branches are somewhat different from those at the periphery (this difference is not simply an effect of foreshortening). It would be pardonable for a worker unacquainted with the history of this colony to mistake figs. 6 and 7 for photographs of distinct species.



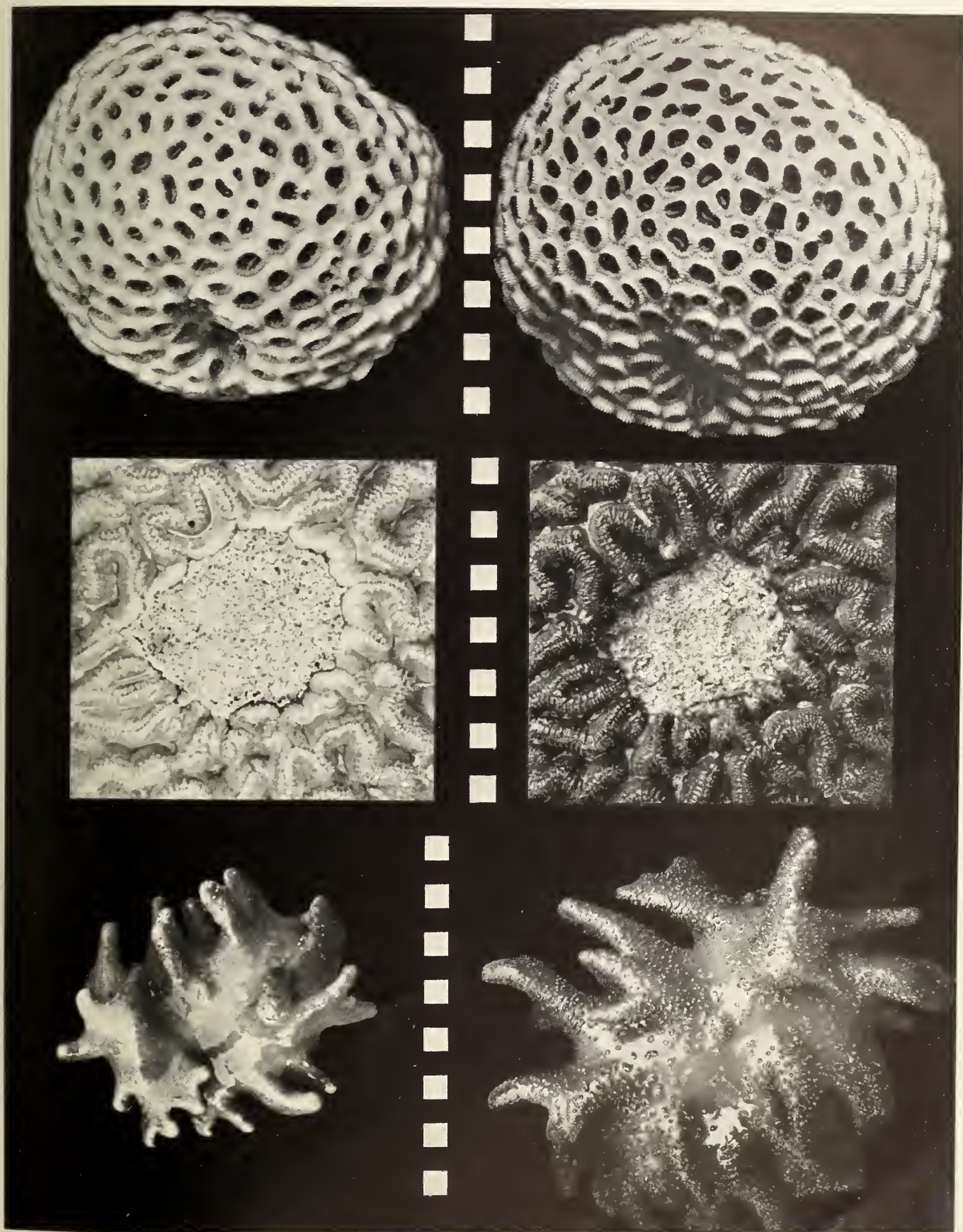
DESCRIPTION OF PLATE VI.

TO ILLUSTRATE SPECIAL POINTS.

FIGS. 1 and 2.—*Favia doreyensis*. Experiment I, no. 70. Collected and planted out in the moat. These figures illustrate the work described on pp. 191-4, in which the history of individual polyps was followed; it will be noted that the fate of each polyp can be traced clearly in the central parts of these two photographs; on original prints, larger than the reproductions, the details are well brought out. The increase in size of the colony was 8% on each of two diameters in 33 weeks 1 day.

FIGS. 3 and 4.—*Symphyllia recta*. Experiment I, no. 11. Collected and planted out in the moat. These figures illustrate part of a large colony which had a dead area in the middle of its upper surface. During the experiment the living part grew inwards over part of the dead region.

FIGS. 5 and 6.—*Lobophytum* sp. Experiment I, no. 24b. Collected and planted out in the moat. To illustrate growth and change of form in one of fleshy alcyonaria which are common on the reef. This specimen grew well in the moat, but the latter cannot be regarded as its normal habitat.



DESCRIPTION OF PLATE VII.

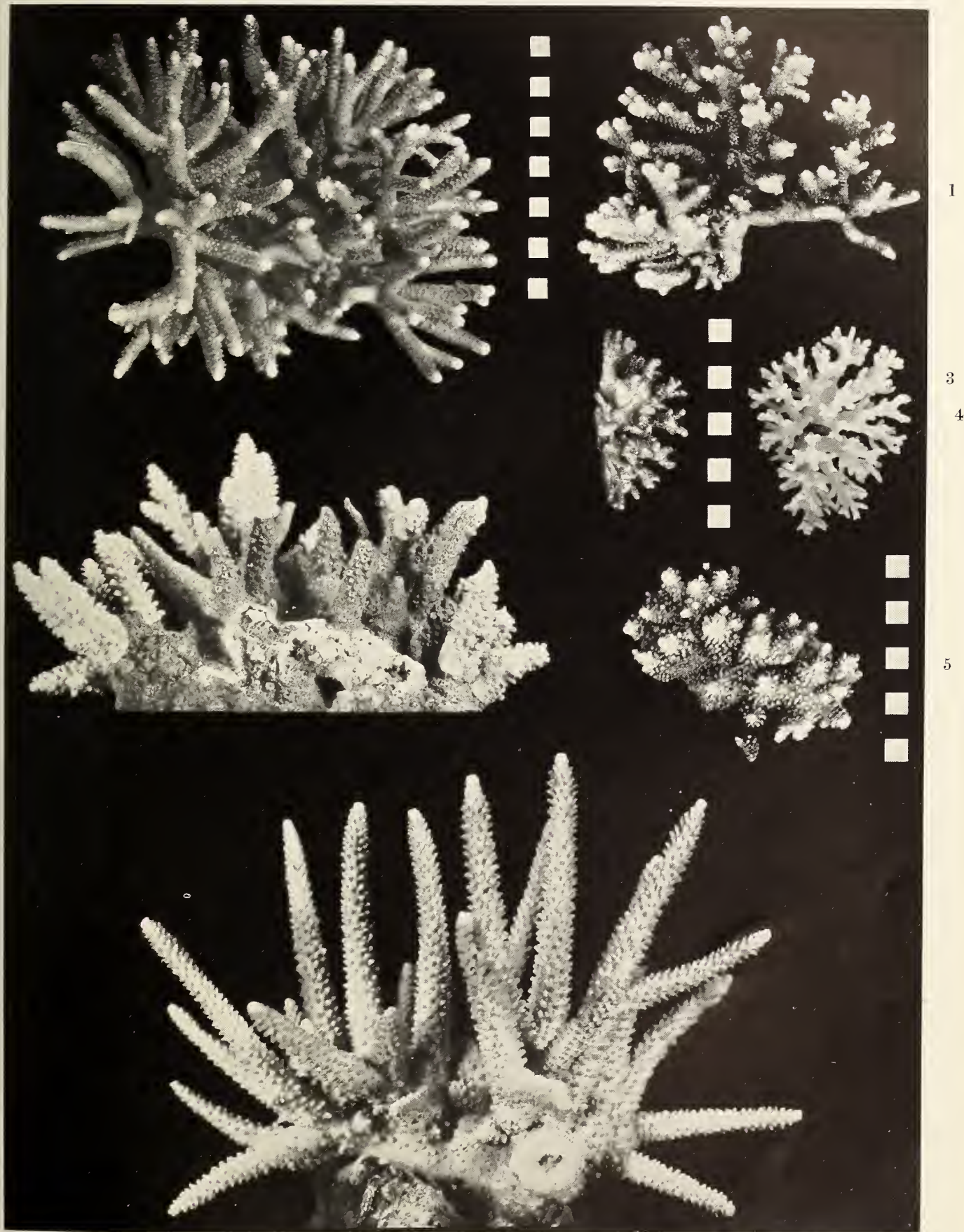
THE EFFECT OF ENVIRONMENT ON GROWTH.

REGENERATION IN POCILLOPORA.

FIGS. 1 and 2.—*Acropora hebes*. Experiment II, no. B 8. Collected and planted out in the moat. This specimen is one half of a colony, the other half of which was planted in the anchorage. Both halves grew well, but the half in the anchorage was broken and could not be measured; the half illustrated increased 59% and 45% on two diameters in 31 weeks 3 days. This species is capable of rapid growth under the rigorous conditions of the moat, which is one of its normal habitats; but it grows well also in the less extreme environment of the anchorage. The aspect of the branches of the specimen illustrated has changed markedly during the experiment.

FIGS. 3 and 4.—*Pocillopora bulbosa*. Experiment II, no. A 4. Collected and planted out in the moat. Fig. 3 represents one half of a young colony which was bisected. The bisection left this half with one particularly flat side. In fig. 4 the colony has regained normal symmetry. See also p. 188.

FIGS. 5-7.—*Acropora* sp. Experiment II, nos. A 7 and B 7. Fig. 5 shows one half of a small colony which was found as a casual in the moat (it was certainly not a normal inhabitant of the latter), and which was bisected. The half illustrated was planted in the anchorage, where it grew very strongly, its appearance at the end of the experiment being represented in fig. 7. The other half, very similar to fig. 5 in appearance, was planted in the moat; its aspect after the experiment is represented in fig. 6; a certain amount of growth has taken place, but much less than in fig. 7, and the branches are all dead at the base, and some of them all the way up. If the experience of this colony is general, the inability of the species to flourish under moat conditions is clearly demonstrable.



DESCRIPTION OF PLATE VIII.

REGENERATION IN ACROPORA.

(See also p. 185.)

FIG. 1.—*Acropora formosa*. Experiment III, no. 2. The tip of a branch which had been allowed to regenerate for 7 weeks 1 day. The broken end was still flat, but the central polyp had regenerated, and was surrounded by a ring of still smaller ones. The skeletal counterparts of these polyps are visible in the photograph. $\times 2$.

FIGS. 2-5.—*Acropora polymorpha*. Experiment III, no. 9. Stages in the regeneration of branches, all more advanced than the early condition shown in fig. 1. The point at which the fracture was made, in each branch, is indicated by a white arrow; and the stages are further described on p. 186. All four branches had been regenerating *for the same period*, viz. for 25 weeks 3 days; all belonged to the same colony and were broken on the same day; yet the amounts of new growth achieved are very different. All figures $\times 2$.

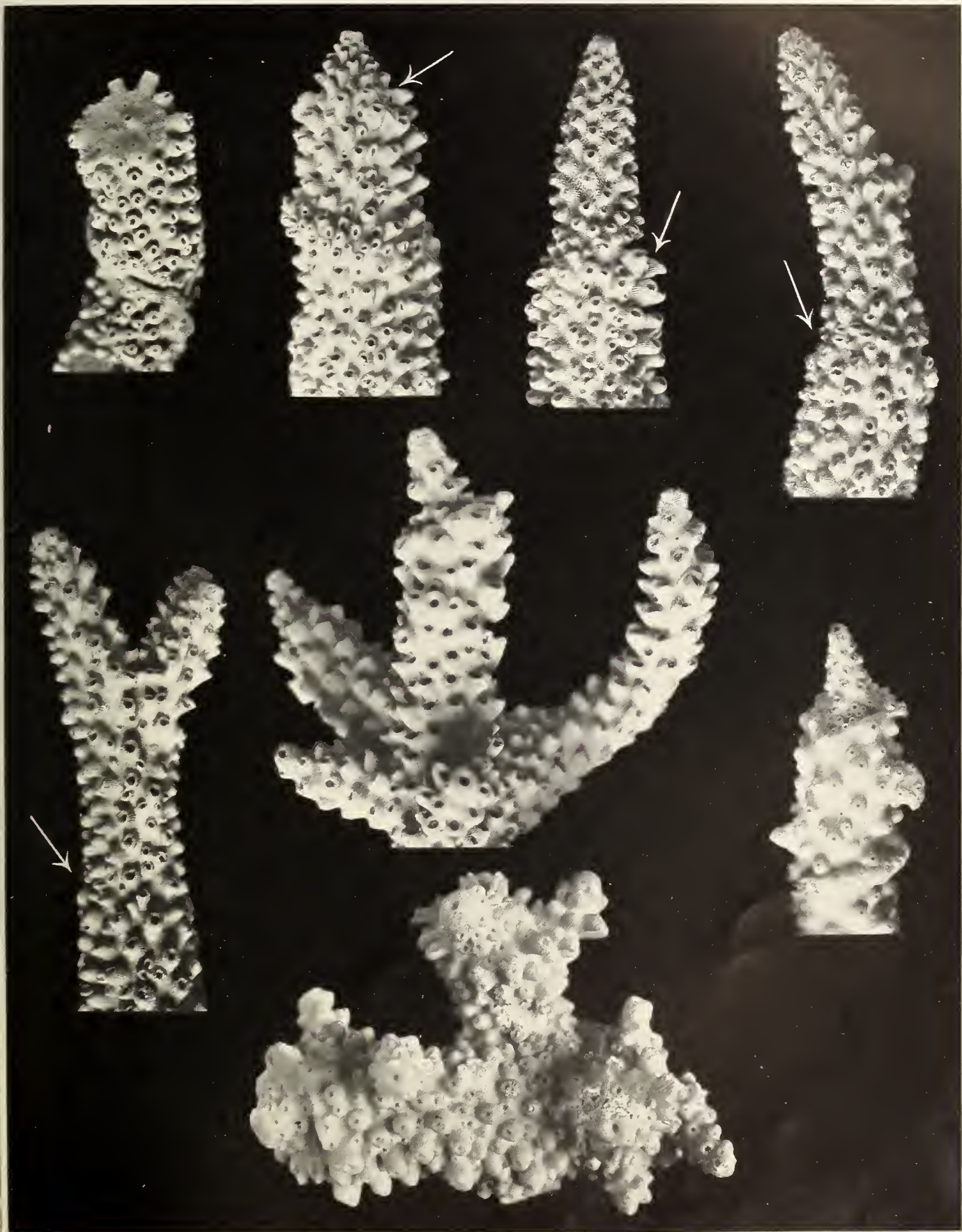
FIGS. 6-8.—These figures illustrate further details of regeneration in species of *Acropora*, and are described on p. 186. All $\times 2$. They belong to Experiment III, nos. 10, 3 and 11 respectively.

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DESCRIPTION OF PLATE IX.

REGENERATION IN ACROPORA.

GROWTH-FORMS ON THE OUTER BARRIER.

FIG. 1.—*Acropora gemmifera*. Experiment III, no. 5. A colony in which a group of branches (on the left-hand side of the figure) was broken off, the colony being left *in situ* to regenerate. The broken branches were marked by a silver wire encircling their bases (the wire is visible in places, in the figure, and has been sheathed with calcium carbonate by the coral). The broken branches, after 13 weeks 5 days, have grown new tips, but are still shorter than the unbroken branches on the right-hand side of the colony. Actual diameter of the colony 42 cm.

FIGS. 2-4.—These figures represent corals growing *in situ* on Yonge Reef, Outer Barrier. Fig. 2 was taken in the outer moat, fig. 3 near the outer ridge, both situations being exposed to strong wave-action at certain states of the tide; fig. 4 was taken on a coral head on the leeward side of the reef. Fig. 2 shows a colony of a small massive species of *Pocillopora* (*P. verrucosa*) which is very characteristic of the region, and is bright magenta in colour; and also an encrusting sheet of *Acropora* (right-hand side of figure) belonging to one of the shelf-like species, probably *A. hyacinthus*, but showing reduction of the branches in correlation with the encrusting habit. Fig. 3 shows a case of the reduction of branches to conical prominences. The species is probably *A. gemmifera*, the one also illustrated in fig. 1, which represents a colony from a sheltered habitat at Low Isles. Fig. 4 (also *A. gemmifera*) shows the variation in the form of individual branches which may occur in one and the same colony. The branches in the centre are short and conical (the effect of foreshortening in this case is relatively slight), whilst those round the edge of the colony are comparatively slender and finger-like, and are comparable to the ones illustrated in fig. 1.

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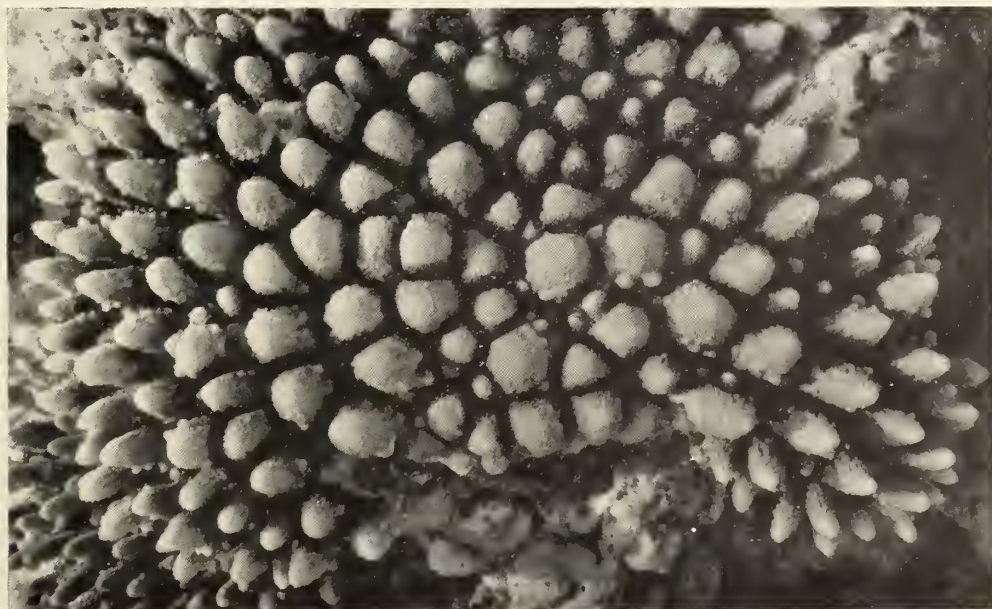
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*Fig. 1 photographed by F. Pittock.
Fig. 2-4 photographed by S. M. Manton.*

DESCRIPTION OF PLATE X.

HABITAT AND GROWTH-FORM IN ACROPORA.

FIGS. 1 and 2.—*Acropora squamosa*. These figures represent portions collected by S. M. Manton from different sides of the *same colony*. Fig. 1 shows a normal branch of the species, such as would occur on many typical colonies; the branches represented in fig. 2 are so much modified that their recognition as examples of *A. squamosa* would be difficult if their origin were unknown. The colony from which both specimens were taken was growing on the reef-crest of one of the reefs of the Outer Barrier. (The manner in which two growth-forms such as these may grade into each other is shown in Plate IX, fig. 4.) These illustrate a case of marked variation in the form of branches in the *same environment*.

FIG. 3.—A colony (probably referable to *A. gemmifera*) with branches of an intermediate degree of stoutness. Locality unknown.

FIG. 4.—*Acropora squamosa*. From the reef crest, Yonge Reef. A good example of a squat form of the species, which has nevertheless not assumed the atypical appearance of fig. 2.

FIG. 5.—*Acropora gemmifera*. A colony with short and stumpy branches, intermediate between the conditions shown in Plate IX, figs. 1 and 3. The specimen came from the wave-washed pavement at the seaward edge of Batt Reef.

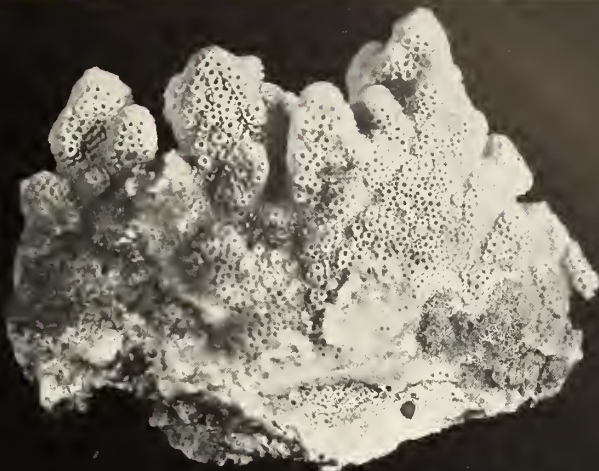
FIG. 7.—*Acropora delicatula*. From the outer moat, Yonge Reef. This species, notwithstanding the fact that its branches are so fragile that it is difficult to collect a colony without breaking it, is a form characteristic of the seaward parts of Yonge Reef, and grows on the outer ridge. Although it is commonest on the sides of clefts where the force of the breakers may be somewhat diminished, it also occurs on the open ridge, where it must at certain times receive their full force. A comparison of this figure with Plate IX, fig. 3, will show how two extremes of structure (depending for strength upon different principles) may both be successful in resisting the pounding of the surf—short cones of great strength on the one hand, which are difficult to split even with a cold chisel; slender fragile branches on the other, which snap off at the least tap from a chisel.

FIG. 6 and 8.—*Acropora hyacinthus*. Fig. 6 shows a typical slender-stemmed example of the species, growing in a sheltered habitat at Low Isles (this specimen was no. 60*b* in Experiment I—see also Plate II, figs. 5 and 6). Fig. 8 shows a stouter colony from the outer ridge on Yonge Reef. These two were growing therefore in habitats exhibiting something approaching the maximum possible amount of difference between shelter and exposure; yet the difference between them is not very marked.

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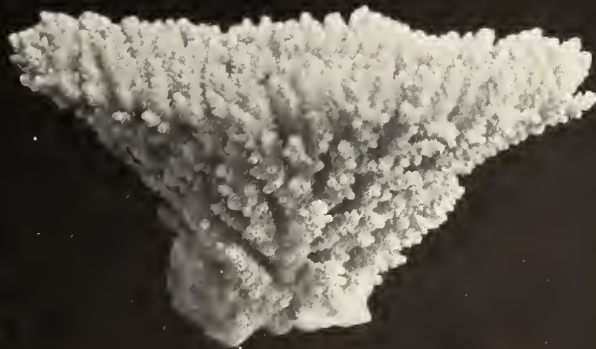
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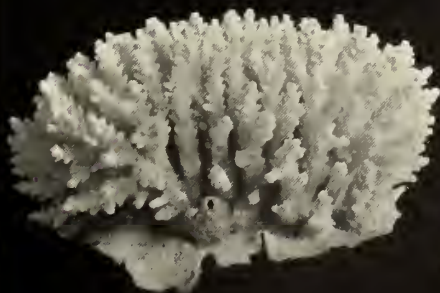
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